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SOIL BIOLOGY AS RELATED TO LAND USE PRACTICES

Proceedings of the VII International Soil Zoology Colloquium of the International Society of Soil Science (ISSS)

Daniel L. Dindal, Editor

1980

Organized by the State University of New York, College of Environmental Science and Forestry.
Held in Syracuse, New York USA, July 29 — August 3, 1979

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PREFACE

In 1976, at Uppsala, Sweden while attending the VIth Colloquium, I extended an official invitation from the State University of New York College of Environmental Science and Forestry (SUNY CESF) to commence the VIIth International Colloquium on Soil Zoology on our campus. This invitation was graciously accepted.

Organizational plans were quickly underway for the meeting to be held in Syracuse in 1979. From July 29 through August 3 of that year, 135 people, interested in various facets of soil biology, met in a very scholarly and congenial atmosphere. Twenty-seven countries from around the world were represented with representatives from five Canadian Provinces and nineteen states from the US on hand.

Being able to organize and take part in such a prestigious conference on our campus has been one of the highlights of my career. And the interest, cooperation and eager participation by all attendees helped make the colloquium so successful.

Of course, one of the main values of such an international meeting is the timely production of the published proceedings. Through the cooperation of the Office of Pesticides and Toxic Substances of the USEPA this objective was realized.

As editor of these proceedings, I compiled and organized the papers in a subject-related manner. Most of my editorializing was of a mechanical nature. A proceedings should be as accurate a reflection of the papers presented as possible. Therefore, no papers were deleted even though some readers may feel the manuscripts lack quality. Each paper as part of the conference helped to develop the character of the total meeting and was, for this reason, included.

All participants were initially given a format to follow in preparation of their papers. In general, most followed these directions very closely for which I am appreciative. Abstracts were optional so they may or may not be present.

It has been a pleasure dealing with all the participants.

Daniel L. Dindal
Syracuse, NY
May 1, 1980

ACKNOWLEDGMENTS

My appreciation is extended to the staff of the School of Continuing Education, under the direction of Dr. John M. Yavorsky, for valuable assistance with all aspects of planning for the meeting facilities, dining and living quarters and field trip arrangements. As the participants will recall, the unwavering energy exhibited by Alan L. Hankin was extraordinary. Also, Dr. John F. Simeone, chairman of the Department of Environmental and Forest Biology deserves thanks for his help, interest and participation. Bruce G. Stevenson and James McIlvain were very diligent in gathering and recording the questions and answers of each speaker. Jeffrey Waugh volunteered his services as a driver for the field trip, and Michael S. Fisher very professionally acted as the chauffeur for the special trips organized for wives of attendees.

Finally, I acknowledge all the invaluable assistance of my wife, Anna Jean Dindal. In addition to her involvement in the conference organization and organizing and guiding the accompanying women's program, she was truly a major factor behind getting these proceedings compiled and produced. Publication at this time would have been impossible without her.

OFFICIAL WELCOME

Donald F. Behrend

Vice President of Program Affairs
SUNY CESF, USA

Good morning and welcome to the Seventh International Soil Zoology Colloquium. Both Chancellor Wharton and President Palmer join me in welcoming you to the State University of New York College of Environmental Science and Forestry.

We are pleased and honored that you have chosen to meet here to pursue the theme of soil biology as related to land use practices. This theme, being followed by scientists from 30 nations around the world, may be viewed as a microcosim of our entire College. Thus, in the CESF we are consciously striving to understand the basis for our environment, how our environment causes impacts on us and how we cause impacts on it; and, how we can modify our utilization of the resources provided by our environment in order to maintain its diversity, stability, and long term productivity.

Soil is, of course, one of the absolutely crucial elements of the system we call our environment. As a practicing wildlife biologist, I appreciated this many years ago; but in an extremely simplistic way. Along with many others, I viewed soil as a relatively simple system of physical and chemical constituents which supported plant life which, in turn, supported, either directly or indirectly, vertebrate animals, and harbored some troublesome parasites. Now, thanks to your continuing investigations, a broad array of scientists, land managers, and policy makers are fast becoming aware of the complex and fragile nature of the soil systems which are an integral part of the spaceship earth on which we are all fellow journeyers.

I am particularly heartened by the broad scope of your deliberations this week as evidenced by the 9 sessions in your program. In addition to basic soil ecology, a perusal of the program indicates that areas from the arctic to the tropics are covered, along with agricultural, silvicultural, mining, and other specific land uses. Additionally, it is encouraging to see the critical areas of pesticides and human waste disposal included in the program. Another topic which needs increasing attention is the impact of chemical contamination on soil communities and the potential role of these communities in decontaminating soils.

It seems to me that the recent recognition of the broader and more complex role of soil in supporting our environment has set the stage for even greater strides in soil biology. Environmental quality, agriculture, forestry, non-renewable resource extraction and associated land reclamation, energy production from biomass (including heat from decomposition), are some of the areas of study which immediately come to mind.

How rapidly you may make strides in these and other areas depends to a large degree on your overall approach. I think it is essential that the context you create, the perspective you project be truly ecological in nature. This will permit you to communicate more effectively with scientists from other disciplines and with managers and policy makers. You should also strive to make clear the relationships of basic research to the future application of knowledge to the problems of both today and tomorrow. Finally, we must all work together to find timely and effective means to communicate the results of your work to a broad array of audiences.

The program of the Seventh International Soil Zoology Colloquium clearly indicates that you are well along the way toward these goals and objectives. I hope that your efforts here this week will be successful in moving you even farther and faster. And with the continuing attention of Dr. Dindal, Dean Yavorsky and my other College colleagues, I am certain that your stay with us will be pleasant as well as productive.

Again, thank you for honoring us with your visit; and, again, welcome to the SUNY College of Environmental Science and Forestry.

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SESSION I: INFLUENCE OF PESTICIDES ON SOIL ORGANISMS

Moderator: C. A. Edwards

Rothamsted Experimental Station
Harpenden, England

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INTERACTIONS BETWEEN AGRICULTURAL PRACTICE AND EARTHWORMS

C. A. Edwards

Rothamsted Experimental Station
Harpenden, England

INTRODUCTION

There are earthworms in most agricultural soils in both temperate and tropical regions, although the species may differ in different parts of the world. The conversion of natural forest or prairie into a regularly cultivated system involves considerable changes in the soil as a habitat so that species that can withstand repeated soil disturbance and a relatively limited supply of organic matter, are favoured at the expense of those that cannot.

Since the publication of Charles Darwin's book, 'The Formation of Vegetable Mould Through the Action of Worms' (1881), there have been many reports that earthworms are important in breaking down plant organic matter and incorporating it into soil, forming soil aggregates and improving soil structure, aeration and drainage. There have also been reports that earthworms improve mineral availability and general soil fertility (Edwards and Lofty, 1977, 1979). Nevertheless, there has been relatively little discussion as to how this is achieved nor how the various forms of agricultural practice affect earthworm populations and, conversely, how earthworms influence the growth of crops. Work on these subjects has been in progress at Rothamsted since 1961 and this paper summarizes some of the main findings of this programme and relates them to the requirements of modern agriculture.

METHODS

The field experiments in which the influence of agricultural practice on earthworm populations have been assessed, all involved small plots (ranging from five metres square to 30 m x 10 m) usually replicated four times. The experimental cultivations, strawburning, and applications of fertilizers and pesticides to these experiments have all followed normal agricultural practice and used recommended doses and timing of treatments.

Earthworm populations were assessed on the basis of four half metre square quadrats per plot (usually a total of 4 m^2/ for four plots). On to each quadrat, 9.2 l of water containing 50 ml formaldehyde were poured gradually from a watering can and the earthworms coming to the surface of the quadrat removed and stored in 5% formalin until they could be weighed and identified to species.

The effects of pesticides and fertilizers on earthworms and, in particular, uptake of chemicals into earthworm tissues have also been assessed in laboratory box tests. These tests have involved setting up cultures of ten earthworms (usually *Lumbricus terrestris* L. or *Allolobophora caliginosa* Savigny) in medium clay loam sterilized soil, contained in boxes 25 cm square and 40 cm deep, kept at 25% moisture content and 15°C (Edwards, 1979). To assess the effects of fertilizers and pesticides, the chemicals were mixed thoroughly into the soil before the worms were added; the boxes were dismantled and mortality assessed at 1 - 2 weekly intervals.

Some experiments have involved the inoculation of earthworms into field sites to study their effects, and to do this the earthworms were spread evenly over the surface of small plots and covered with a large polythene sheet for 24 hours until they had burrowed into the surface soil. There was virtually no lateral migration from these small plots and very good survival of the worms.

RESULTS AND DISCUSSION

1. Effects of pesticides

The literature on effects of pesticides on earthworms has already been reviewed thoroughly (Davey, 1963; Edwards and Thompson, 1973; Edwards and Lofty, 1977) and will not be considered here, except where results disagree with those obtained at Rothamsted.

Pesticides can kill earthworms and can also accumulate in worm tissues. Moreover, earthworms can move pesticides absorbed in their tissues from the soil surface into deeper soil where most of the pests live, thereby often increasing the effectiveness of the pesticide. Some pesticides are degraded within the tissues of earthworms; for instance, even the most stable pesticide, DDT becomes degraded to DDE in earthworms (Edwards and Jeffs, 1974).

Fortunately, most pesticides do not kill earthworms at normally recommended doses, which makes it even more difficult to have some assessment of the relative toxicity of different pesticides to them. The relative toxicity of a wide range of pesticides to earthworms is summarised in Table 1 which is an overall assess-

TABLE 1 RELATIVE TOXICITY OF PESTICIDES TO EARTHWORMS

Chemical	Use	Relative toxicity to earthworms
Chloropicrin	Nematicide	* * * * *
D-D	"	* * * * *
Methyl bromide	"	* * * * *
Metham sodium	"	* * * * *
Aldicarb	"	* * *
Dazomet	"	* *
Thionazin	"	* *
Methomyl	"	* *
Chlordane	Organochlorine insecticide	* * * * *
Endrin	"	* * * *
Heptachlor	"	* * *
DDT	"	0
Dieldrin	"	0
Aldrin	"	0
BHC (lindane)	"	0
Phorate	Organophosphate insecticide	* * * * *
Parathion	"	* * *
Fonofos	"	* *
Trichlorphon	"	*
Fenitrothion	"	0
Tetrachlorvinpos	"	0
Disulfoton	"	0
Malathion	"	0
Menazon	"	0
Chlorfenvinphos	"	0
Carbaryl	Carbamate insecticide	* * * * *
Carbofuran	"	* * * * *
Benomyl	Carbamate fungicide	* * * * *
Thiophanate methyl	"	* * * * *
Carbendazim	"	* * * * *
Methiocarb	Carbamate molluscicide	* * *
Simazine	Herbicide	* *
Cyanazine	"	* *
Chlorthiamid	"	*
DNOC	"	*
Benzoylpropethyl	"	0
Linuron	"	0
Monuron	"	0
Paraquat	"	0
Dalapon	"	0
Triallate	"	0

* * * * *	Extremely toxic
* * * *	Moderately toxic
* * *	Intermediately toxic
* *	Slightly toxic
*	Very slightly toxic
0	Non-toxic

ment based on both laboratory and field tests. Most nematicides tend to be broad-spectrum biocides and are therefore to varying degrees toxic to earthworms and, in particular, the fumigant nematicides chloropicrin, D - D, methyl bromide and metham sodium are very toxic to worms. Of the organochlorine insecticides, only chlordane is very toxic to earthworms with endrin slightly less so, but these pesticides are readily absorbed from soil into earthworms' tissues, so that there can be as much as ten times the concentration of the chemical in the tissues as in the surrounding soil.

Organophosphate insecticides seem to be the least toxic pesticides to earthworms, only phorate being very toxic with parathion rather less so. Only small amounts of organophosphate insecticides are taken up into earthworm tissues. All of the carbamate pesticides seem to be relatively toxic to earthworms. Most herbicides are not directly toxic to earthworms (only the triazines being slightly toxic) but herbicides have very considerable indirect effects on earthworms by changing the surface vegetation which ultimately provides soil organic matter.

Earthworms are considered to be sufficiently important test organisms for the British Pesticide Safety Precautions Scheme (linked to the registration scheme) to require pesticide firms to provide earthworm toxicity data (Edwards, 1978).

2. Effects of fertilizers

Fertilizers, either organic or inorganic, are applied to most agricultural crops. In some long term experiments at Rothamsted, the same fertilizers have been applied annually to plots of grass, root crops or wheat since the 1840's, in what are termed the 'Classical experiments'. Fluctuations in the earthworm populations in these plots and in other shorter term experiments have demonstrated clearly how fertilizers affect numbers. In all experiments, populations increased after application of dung or fish meal and other organic fertilizers. The deep-burrowing species *Lumbricus terrestris* increased, particularly. Balanced mineral fertilizers containing N, P, K, Na and Ng have caused slight increases but large doses of ammonium nitrogen have decreased earthworm numbers significantly probably because such treatment increases soil acidity (Fig. 1). These conclusions have been supported by

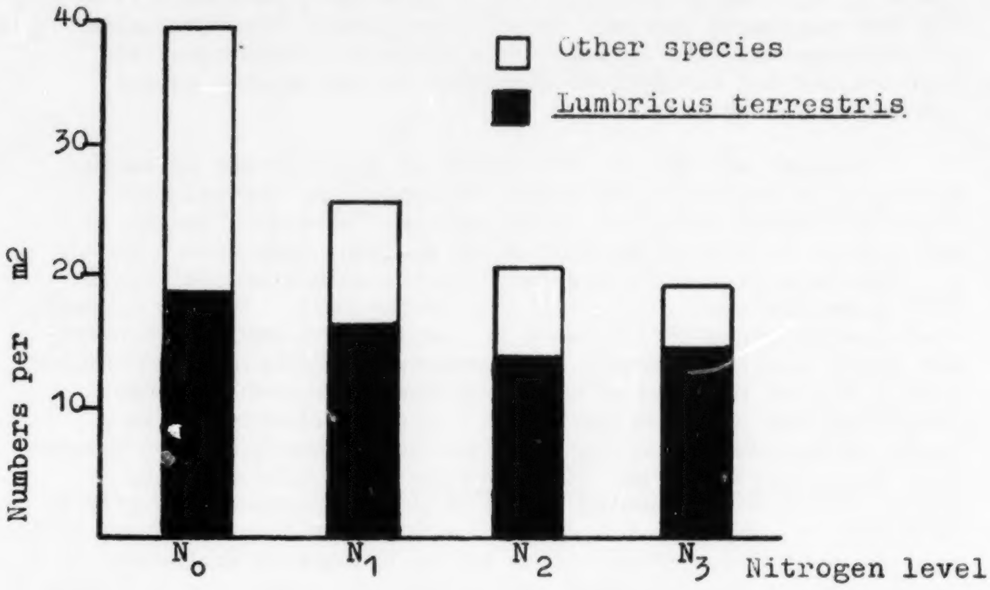


FIGURE 1. EFFECTS OF NITROGEN (AMMONIUM SULPHATE) ON EARTHWORM POPULATIONS (N_1 = 48 kg/ha, N_2 = 96 kg/ha, N_3 = kg/ha)

data from other workers (Edwards and Lofty, 1975b). Other nitrogenous fertilizers, particularly calcium nitrate ('nitro-chalk'), and the addition of lime to soil, favour the build-up of most species of earthworms.

More recently, sewage sludge, sewage cake, animal slurries and waste from breweries have been used as organic fertilizers and our results have shown that although some of the raw forms may kill a few earthworms they usually increase populations, eventually quite considerably. Unfortunately, there can be some uptake of the heavy metals Pb, Zn and Cd into earthworm tissues from the sewage materials.

3. Effects of cultivations

Grassland tends to contain more earthworms than arable land, but it is not certain whether this is due to regular disturbance of the habitat by cultivation or to lower levels of soil organic matter in ploughed fields. An experiment at Rothamsted investigated the effects on earthworm populations of ploughing up old grassland and using either the maximum or minimum additional cultivations before reseeding to grass; the effects of doing this once were compared with those of repeating the cultivations annually. During the first two seasons, the overall earthworm populations increased in all the reseeded plots compared with the uncultivated ones but most of the increase was of the shallow-working species; with repeated reseeding, populations, particularly of the deep-burrowing species, began to decrease. The conclusion was that many species of earthworms could withstand repeated cultivations but populations decreased as the organic matter content of the soil fell.

Investigations into the impact of cultivations on earthworm populations have been given new impetus by the practice known as 'direct drilling' in England and 'no-till' farming in the U.S.A. This involves killing an existing crop with a broad-spectrum herbicide and reseeding directly with a special drill that drops the seed into a slot cut in the soil. This is becoming more popular since 1973 because of considerable savings in energy and labour and also because it minimizes soil erosion; in England half a million hectares of crops are currently sown this way. Investigations at Rothamsted on 24 field experiments and in a field survey have shown that populations of deep-burrowing species such as L. terrestris and Allolobophora longa tend to build up spectacularly with repeated direct drilling, although the effects on numbers of shallow-working species are much less (Edwards, 1975; Edwards and Lofty, 1975a). Some of the changes in earthworm populations in two long term experiments are summarised in Figure 2.

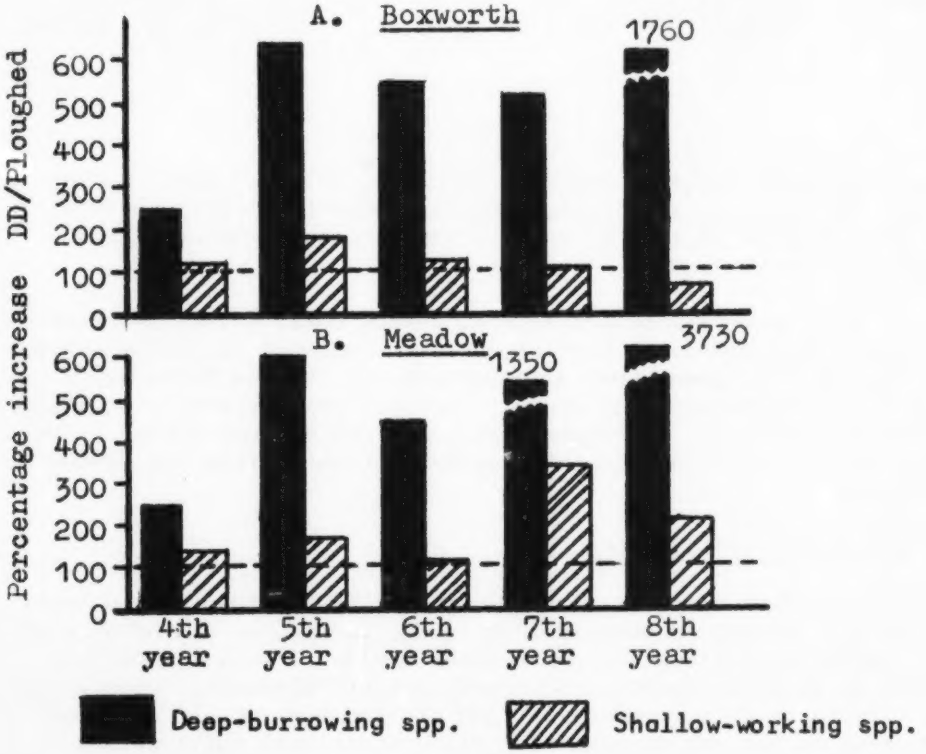


FIGURE 2. RELATIVE CHANGES IN EARTHWORM POPULATIONS RESULTING FROM DIRECT DRILLING

Other experiments in both field and laboratory have shown that earthworms are important in promoting the root growth of direct drilled cereals by providing suitable tunnels and spaces lined with available nutrients in the relatively compacted soil. Moreover, since some earthworm burrows go deeper than the plough pan, roots penetrate deeper than in ploughed soil.

Thus, it has been established that the greater the intensity and frequency of cultivations generally the fewer earthworms are present.

4. Strawburning

The practice of burning straw in cereal fields after harvest is common in England, about 50% of all cereal straw being currently disposed of in this way. The effects of strawburning on earthworm populations has been investigated since 1974 at Rothamsted. In one long-term experiment, the effects of chopping straw and spreading it evenly over some plots were compared with doing the same and burning the straw, baling and removing the straw, and leaving the straw in swathes over the rows and burning it. The burning or removal of straw had little effect on earthworm populations in the first year, a slight effect after the second treatment but, by the third and fourth years, populations of the deep-burrowing L. terrestris had decreased dramatically, and to a lesser extent so had those of the shallow-working A. caliginosa. By contrast, burning favoured populations of Allolobophora chlorotica (Savigny) (Figure 3) (Edwards and Lofty, 1979).

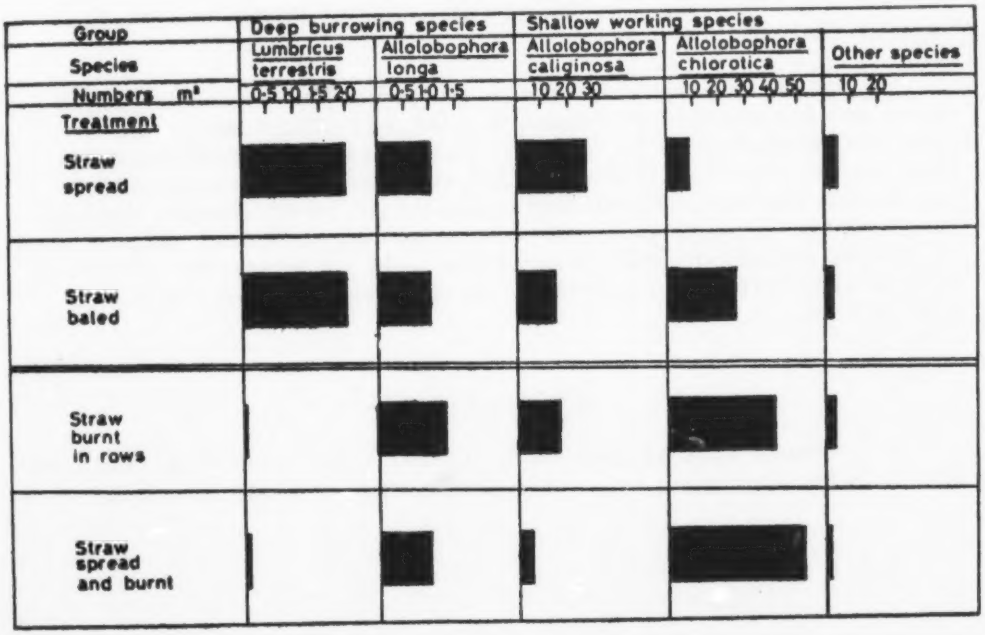


FIGURE 3. THE EFFECTS OF STRAW DISPOSAL ON EARTHWORM POPULATIONS (after three successive years)

There seems little doubt that the actual burning had little effect on earthworms but that populations of those species dependent upon the availability of surface organic matter were soon affected.

5. Rotations

There is very little evidence on the influence of rotations on earthworm populations. However, the data that have been accumulated at Rothamsted, indicate that earthworm populations tend to build up under continuous cereal cropping much more than in three or four course rotations involving such crops as beans, potatoes, oil seed rape or fodder crops. This is presumably because the cereal stubble and roots, which constitute about 50% of the total biomass of the crop plus any straw left on the field, add greatly to the soil organic matter upon which many species of earthworms depend.

6. The management of earthworm populations for maximum agricultural benefit

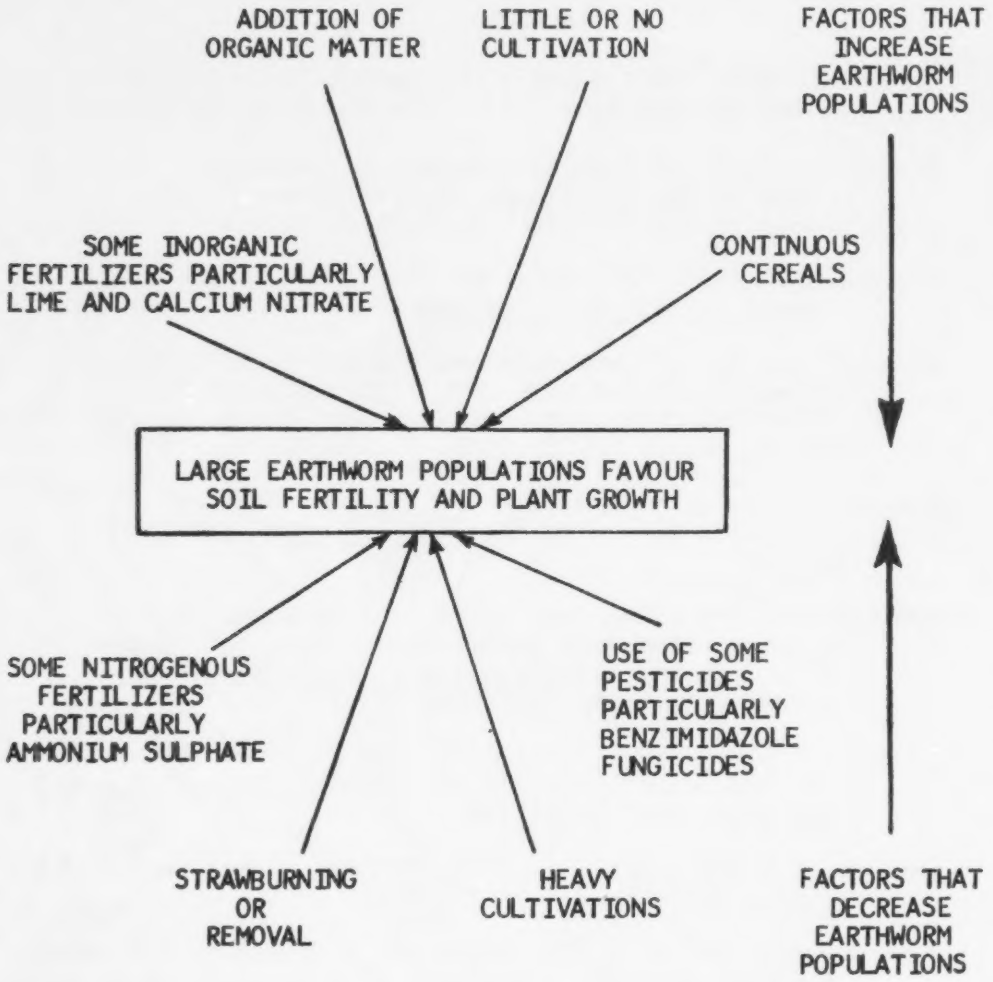
The concensus of evidence is that earthworms improve soil structure, fertility, organic matter decomposition, aeration and drainage. Their importance increases with the current tendency towards minimal or zero cultivation. If this is accepted, there is a strong case for a programme of earthworm management aimed at encouraging practices which favour the build-up of earthworm populations and avoidance, as far as possible, of practices which are harmful to them.

The various agricultural activities which influence earthworms are illustrated in Figure 4. Not all affect earthworm populations equally. In order of importance, they are probably: addition of organic matter, minimal cultivation, strawburning, continuous cereals, use of pesticides toxic to earthworms and use of inorganic fertilizers. We have enough experimental data on most of the parameters in this model to be able to define the optional agricultural practices necessary to encourage maximum earthworm populations.

ACKNOWLEDGEMENTS

I should like to thank J.R. Lofty, B.A. Jones, A.E. Whiting and J. Bater for their extensive assistance in these investigations.

FIGURE 4. MODEL FOR THE MANAGEMENT OF EARTHWORM POPULATIONS


ADDITION OF ORGANIC MATTER
LITTLE OR NO CULTIVATION
FACTORS THAT INCREASE EARTHWORM POPULATIONS
SOME INORGANIC FERTILIZERS PARTICULARLY LIME AND CALCIUM NITRATE
CONTINUOUS CEREALS
LARGE EARTHWORM POPULATIONS FAVOUR SOIL FERTILITY AND PLANT GROWTH
SOME NITROGENOUS FERTILIZERS PARTICULARLY AMMONIUM SULPHATE
USE OF SOME PESTICIDES PARTICULARLY BENZIMIDAZOLE FUNGICIDES
STRAWBURNING OR REMOVAL
HEAVY CULTIVATIONS
FACTORS THAT DECREASE EARTHWORM POPULATIONS

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ACCUMULATION OF ORGANOPHOSPHORUS INSECTICIDES IN EARTHWORMS AND REACTIONS OF EARTHWORMS AND MICROORGANISMS TO THESE SUBSTANCES

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INTRODUCTION

According to Edwards, Lofty (1973), many authors have investigated the effect of pesticides on earthworms and the accumulation of pesticides in the organism of earthworms. Many pesticides that get into the soil are detrimental to earthworms. Fürst and Ronnenberg (1974) mention several pesticides that are being used against rodents and are pernicious to earthworms. Ruppel and Laughlin (1977) analyzed what effect on the organism of earthworms had the pesticides usually applied against nematodes. These authors have observed that the pesticides are less harmful to earthworms if those substances get into the soil in the form of pellets and not in the form of dust. They also established that organophosphorus pesticides are less injurious than the carbomatic ones.

Organophosphorus insecticides are used rather widely, but their effect on the useful fauna such as earthworms as well as on the soil microorganisms is little known.

The aim of our investigations was to elucidate the effect of organophosphorus insecticides on the activity of earthworms, on their survival, the accumulation of organophosphorus insecticides in the organism of earthworms, the densities of soil microorganisms and the specific composition of microscopic fungi.

METHODS

Investigations were carried out in 1977-1978; they were performed in a field (200 m^2) and in a wood (on 0.25 and 12 m^2 plots) both unfertilized and fertilized by leaves and green lupine. Leaves and lupine were put in nylon net sacks; insecticides were inserted there too mixed with the soil. Some part of the investigations was performed in pots which contained 3 kg of soil and had 30 or 50 g of straw or 12 g of leaves and 15 or 20 earthworms (control contained no earthworms).

Investigations were done with 3 repetitions. The following insecticides were investigated: anthio, benzophosphate (phosalone), phosphamide, chlorophos, metatione. (The doses of insecticides are indicated in Table 1).

The following media were used for the cultivation of microorganisms: meat peptone agar (MPA), starch ammonia agar (SAA) and beer mash agar (BMA). The number of microorganisms per gram of absolutely dry soil. The amount of insecticides in the organism of earthworms was calculated following the spontaneous removal of earth from their intestine. Minced earthworms were treated by acetone and analyzed by means of the chromatographic device "Tsvet-5" with thermionic detector; the procedure was repeated twice.

RESULTS

1. The effect of organophosphorus insecticides on the activity of earthworms and their survival.

Anthio, benzophosphate and chlorophos decreased the survival of earthworms in the pots by 33 to 46 per cent as compared with the survival of earthworms without insecticides. Straw mineralization proceeded more slowly when pots with earthworms contained also insecticides (with the exception of chlorophos).In the variants with insecticides earthworm activity was also weaker and earthworms had less effect on the intensity of straw mineralization. In the variant with phophamide (5 mg per 1 kg of soil) earthworms did not survive and straw mineralization proceeded there more slowly by 32.8 per cent. Harmfulness of anthio depended on its amount in the soil. Little doses of anthio (0.7 mg per 1 kg of soil) did not decrease the survival of earthworms (Table 1).

During experiments performed in the wood chemicals (viz. chlorophos 20 and 30 days from the insertion in the soil and benzophosphate 30 and 60 days from its insertion) had a delaying effect on the earthworm migration to the corresponding organic substance.

2. The accumulation of organophosphorus insecticides in the organism of earthworms.

At the beginning of the experiment metathione in the soil was 2.0 p.p.m., but following 20 days from the beginning of the experiment we found in 1 kg of soil 0.2 mg of metathione residue and almost the same amount in the earthworms (in *Eisenia rosea* 0.2 p.p.m. and in *Allolobophora caliginosa* 0.3 p.p.m. At the beginning of the experiment benzophosphate in the soil was 15;150p.p.m., after 65 days the residue of benzophosphate in the earthworms *Lumbricus rubellus* was found 4.8; 2.7; 2.9 p.p.m. (the corresponding amount in the soil was 1.7; 8.2; 20.7 p.p.m.). Earthworms were investigated in the wood where they could freely immigrate and emigrate and therefore their life period in the experiment might be different.

We have found almost the same amounts of dimethoate,

Table 1. EFFECT OF ORGANOPHOSPHORUS INSECTICIDES ON THE ACTIVITY AND SURVIVAL OF ALLOLOBOPHORA CALIGINOSA (in the pots)

Variants and the duration of experiments	Unrotten straw (%) in variants: control	Unrotten straw (%) in variants: with earthworms	Earthworm survival (%)
May-July 1976 (65 days)			
Without chemicals	40.4	32.2	89.0
Phosphamide (5 p.p.m.)	73.2	71.4	-
Benzophosphate (150 p.p.m.)	60.0	56.2	55.0
June-August 1977 (75 days)			
Without chemicals	27.6	16.0	95.0
Benzophosphate (150 p.p.m.)	30.3	21.0	48.0
Chlorophos (80 p.p.m.)	15.6	13.0	60.0
April-September 1978 (130 days)			
Without chemicals	15.0	11.3	86.5
Anthio (1.5 p.p.m.)	14.3	14.6	43.0
Anthio (12.0 p.p.m.)	38.6	36.0	-
Anthio (1.5 p.p.m.) (155 days)	9.7	5.1	40.0
Without chemicals (155 days)[x]			75.0
Anthio (0.7 p.p.m.)[x]			75.0
July-August 1978 (60 days)			
Without chemicals	33.3	31.6	73.5
Anthio (200 p.p.m.)	34.0	32.3	42.0
August-September 1978 (30 days)			
Without chemicals[xx]			88.5
Anthio (200 p.p.m.)[xx]			45.0

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x - fertilized with leaves

xx - unfertilized

the metabolite of anthio, in the organism of Allolobophora caliginosa as in the soil (0.4 p.p.m. and 1.7 p.p.m. respectively; and 0.4 p.p.m.; 0.6 p.p.m. in earthworms and the same amounts in the soil). When bigger amounts of anthio were put in the soil (200 p.p.m.) we have found 7.4 mg of this chemical per 1 kg of soil and 5.8 mg of earthworms following 30 days and 3.2 mg per 1 kg of soil and 1.0 mg per kilogram of earthworms following 80 days from the beginning of the experiment.These data give us sufficient ground to assume that depending upon the time the amount of dimethoate, the metabolite of anthio, both in the earthworms and in the soil is decreasing. A slight amount of anthio was found in the soil(0.1; 0.3 p.p.m.), in the organism of earthworms there were detected only tracks. (Table 2).

Apart from this the accumulation of insecticides in the organism of earthworms does show that on the one hand earthworms accelerate soil purification of these harmful substances and on the other hand earthworms prolong the harmful effect of pesticides when these invertebrates are consumed by birds and other animals.

3. The effect of earthworms and the insecticide anthio on densities of microorganisms.

It is well established that earthworms act positively on the development of microorganisms in the soil (Atlavinytė, Lugauskas, 1973; Atlavinytė, 1975; Brüsewitz, 1959; Ghilarov, 1963; Kozlovskaja, 1969; Went, 1963). In analyzing the present results of these investigations one may clearly see that earthworms in this case too did stimulate the development of microorganisms. In almost all the variants of our investigations microorganisms have considerably multiplied in the soil due to the favourable role of earthworm activity. It has been noted that the densities of actinomycetes and microscopic fungi increased when the insecticide anthio was added to separate variants of our experiment. It may be seen more obviously in the variants without earthworms. The effect of anthio on microorganisms partly depends on its amount and the duration of its action. Earthworms have decreased the effect of anthio on microorganisms(Table 3).

4. The change in specific composition of fungi due to the effect of earthworms and the insecticide anthio.

The results of our investigations have shown that earthworms and the insecticide anthio are powerful ecological factors that influence the change in specific composition of soil fungi. Owing to these factors the succession of microscopic fungi in the soil takes place. Generally the composition of microscopic fungi in the soil is rather constant and changes but little. Most often the same species of fungi are found in all the samples of soil of the same type. It is rarely that dominant spe-

Table 2. RESIDUES OF ORGANOPHOSPHORUS INSECTICIDES AND THEIR ACCUMULATION IN THE ORGANISM OF EARTHWORMS

Insecticides	Surface under investigation, m^2	Duration of experiments, days	Amount of insecticides in the soil at the beginning of the experiments, p.p.m.	Residues of insecticides, p.p.m.		The species of earthworms
				in the soil	in the earthworms	
Metathion	200	20	2.0	0.2	0.2	Eisenia rosea
					0.3	Allolobophora caliginosa
Benzophosphate	12	65	15.0	1.7	4.8	Lumbrious rubelius
"	12	65	150.0	20.7	2.7	" "
"	0.25	65	150.0	8.2	2.9	" "
"	in the pot	65	1700.0	n	5.6	" "
Anthio*	"	65	140.0	1.7*	1.4*	Allolobophora caliginosa
"	"	155	0.7	0.4*	0.4*	" "
"	"	155	1.5	0.6*	0.6*	" "
"	"	80	200.0	0.1	1.0*	" "
				3.2*		" "
"	"	30	200.0	0.3	t.	" "
				7.4*	5.8	" "

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* - Dimethoate, the metabolite of anthio, found in the earthworms and the soil.
n - not investigated; t - track

Table 3. EFFECT OF EARTHWORMS AND THE INSECTICIDE ANTHIO ON THE DENSITIES OF MICROORGANISMS IN THE SOIL UNFERTILIZED AND FERTILIZED BY STRAW AND LEAVES (1978)

Variants and the duration of experiments	Unrotten straw (%)	Densities of microorganisms (in thousands per 1 g of soil)		
		MPA	SAA	BMA
April-September (130 days)				
Control	15.0	134.8	427.0	67.4
20 earthworms	11.3	362.6	600.0	76.9
Control + 1.5 mg of anthio per 1 kg of soil	14.3	172.4	780.0	298.8
20 earthworms + 1.5 mg of anthio per 1kg of soil	14.6	400.0	621.2	70.6
20 earthworms + 0.7mg of anthio per 1 kg of soil (150 days)	*	321.4	535.7	95.2
July-September (60 days)				
Control	33.3	800.0	124.0	119.6
15 earthworms	31.6	420.0	2043.0	150.5
Control + 200 mg of anthio per 1 kg of soil	34.0	472.5	1208.8	87.9
15 earthworms + 200 mg of anthio per 1 kg of soil	32.3	1068.2	1931.8	125.0
15 earthworms + 200 mg of anthio per 1 kg of soil (80 days)	31.3	1101.1	1180.0	78.7
August-September (30 days)				
20 earthworms	* *	483.6	714.3	142.9
20 earthworms + 200 mg of anthio per 1 kg of soil	* *	160.0	750.0	181.8

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* - fertilized with leaves

* * - unfertilized

cies of fungi would chnage in the soil. As we see from Table 4, however, the specific composition of dominant fungi did change very much owing to the effect of earthworms and the insecticide anthio. Due to the above-mentioned reason the formerly formed association of soil fungi disintegrate, their functional activity is impaired and new favourable conditions appear for the intensive development of other fungi species the activity of which was earlier inhibited by the development of former dominant species of fungi.

Table 4. EFFECT OF EARTHWORMS AND THE INSECTICIDE ANTHIO ON THE DISTRIBUTION OF DOMINANT MICROSCOPIC FUNGI IN UNFERTILIZED SOIL AND THE SOIL FERTILIZED WITH STRAW AND LEAVES (1978)

Variants and the duration of experiments	The number of species	Dominant species
April-September (130 days)		
Control	20	Hormiactis candida v.Höhnel Acremonium roseum (Oud.) W.Gams Trichoderma hamatum (Bon.) Bain. T.viride Pers.ex S.F.Gray Scopulariopsis fusca Zach Penicillium subleteritium Biourge P. canescens Sopp P. terlikowskii Zal. Mycelia sterilia
20 earthworms	18	Mortierella candelabrum v.Tiegh et Le Monnier M. humilis Linnem. M. alpina Peyronel Trichoderma hamatum (Bon.) Bain T. viride Pers. ex S.F.Gray Acremonium butyri (v.Beyma)W.Gams Penicillium purpurogenum Stoll P. nigricans (Bain.) P. luteum Zukal P. miczynskii Zal. Fusarium redolens Wr. Mycelia sterilia
Control + 1.5 mg of anthio per 1 kg of soil	29	Penicillium lanosum Westl. P. capsulatum Raper et Fennell P. godlewskii Zaleski Trichoderma viride Pers.ex S.F.Gray Myrothecium verrucaria Difmar ex Fr. Cladosporium herbarum Link ex Fr. Alternaria alternata (Fr.) Keissl

Table 4 (Ctd.)

Variants and the duration of experiments	The number of species	Dominant species
		Oospora lactis (Fres.) Sacc. Verticillium album (Preuss) Pidopliczko Mycelia sterilia
20 earthworms + 1.5 mg of anthio per 1 kg of soil	21	Mortierella vinacea Dixon-Stewart Penicillium cyclopium Westl. P. godlewskii Zaleski Oidiodendron tenuissimum (Peck) Hughes Acremonium roseum (Oud.) W.Gams Mucor plumbeus Bon. Mycelia sterilia Paecilomyces javanicum Brown ex Smith
20 earthworms + 0.7 mg of anthio per 1 kg of soil (150 days) *	17	Aspergillus niger v.Tieghem Mortierella humilis Linnem. Gonytrichum macroeladum (Sacc.) Hughes Penicillium roseo-purpurogenum Dierckx P. capsulatum Raper et Fennell P. godlewskii Zaleski Paecilomyces javanicus Brown ex Smith Mycelia sterilia
July-September (60 days)		
Control	32	Trichoderma viride Pers. ex S.F.Gray T. hamatum (Bon.) Bain. Penicillium restrictum Gilman et Abbott P. godlewskii Zaleski Syncephalastrum racemosum Conh ex Schraet. Mortierella lignicola (Martin) Gams et Moreau Cephalosporium sp.sp. Humicola fuscoatra Traaen Gliocladium album (Preuss) Petch Papularia sphaerosperma (Pers.) v.Höhnel Oidiodendron tenuissimum (Peck) Hughes
15 earthworms	22	Mucor circinelloides v.Tiegh. Absidia spinosa Lendn.

Table 4 (Ctd.)

Variants and the duration of experiments	The number of species	Dominant species
		Acremonium strictum W.Gams ined. Trichoderma viride Pers. ex S.F.Gray Penicillium godlewskii Zaleski P. purpurogenum Stoll P. simplicissimum (Oud.) P. canescens Sopp P. restrictum Gilman et Abbott
Control + 200 mg of anthio per 1 kg of soil	19	Actinomucor corymbosus (Harz) Naumov Mucor humilis Naumov Mortierella alpina Peyronel M. lignicola (Martin) Gams et Moreau Trichoderma hamatum (Bon.) Bain Penicillium restrictum Gilman et Abbott P. purpurescens (Sopp) Raper. P. decumbens Thom Cladosporum herbarum Link ex Fr.
15 earthworms + 200 mg of anthio per 1 kg of soil	30	Aspergillus fumigatus Fres. Rhizopus oligosporus Saito Penicillium godlewskii Zaleski P. cyaneum (Bain. et Sart) Biourge P. decumbens Thom Mucor plumbeus Bon. M. circinelloides v.Tiegh. Acremonium roseum (Oud.) W.Gams Mycelia sterilia
15 earthworms + 200 mg of anthio per 1 kg of soil (80 days)	16	Penicillium godlewskii Zaleski P. terrestre Jensen P. subleteritium Biurge P. corylophillum Dierckx Sporotricum clivaceum Fr. Trichoderma aureoviride Rifai Mycelia sterilia
August-September (30 days)		
20 earthworms[xx]	16	Mortierella polycephala Coem. Sporotrichum clivaceum Fr. Penicillium restrictum Gilman et Abbott P. decumbens Thom P. javanicum v. Beyma Cephalosporum curtipes Sacc. Acremonium roseum (Oud.) W.Gams

Table 4 (Ctd.)

Variants and the duration of experiments	The number of species	Dominant species
		Mucor griseo-ochraceus Naumov Mycelia sterilia
20 earthworms + 200 mg of anthio per 1 kg of soil **	19	Penicillium decumbens Thom P. piscarium Westl. P. subleteritium Biurge P. simplicissimum (Oud.) Gliomastix cerealis (Karst.) Dickinson Paecilomyces javanicum Brown ex Smith Mycelia sterilia

It was noted that earthworms and caproliths produced by them stimulate the development of the fungi Mucorales. In the variants with earthworms there was an increase in the development of such genera of soil fungi as Mortierella, Mucor, Actinmucor, Absidia, Rhizopus.

In the soil fertilized by straw the fungi of the genus Trichoderma (T. hamatum, T.viride, T.aureoviride and others) and also some representatives of the genus Penicillium (P. capsulatum, P.godlewskii, P.purpurogenum) developed more intensely.

Due to the effect of anthio sterile mycelium of fungi increased in the soil samples; when sown into nutritive media under normal laboratory conditions this mycelium did not produce organs of reproduction. Meanwhile in separate cases the sterile mycelium copiously produced and excreted into the environment its enzymes and acids. Separate strains of the sterile mycelium when acted upon by special means acquired capacity to produce organs of reproduction. But the latter strains of fungi and their organs of reproduction differed greatly from the standard strains of the same species of fungi. Thus it was established that the insecticide anthio may have a negative effect on the development of separate species of fungi and limit their distribution in the soil. However, not all species of fungi react equally sensitively to this chemical. Some species of the fungi belonging to the genus Penicillium under the effect of anthio intensify their activity and become very competitive (P. godlewskii, P.canescens, P.mirczynskii).

SUMMARY

Organophosphorus insecticides, such as anthio, benzophosphate (phosalone) and chlorophos, have decreased the survival of earthworms up to 46 per cent. Anthio, benzophosphate weakened the activity of earthworms and slowed the mineralization of organic substances. The following residues of accumulated insecticides were found in the tissues of earthworms: 0.2 to 0.3 p.p.m. of metathione, 2.7 to 5.6 p.p.m. of benzophosphate and 0.4 to 5.8 p.p.m. of dimethoate, the metabolite of anthio, per 1 kg of earthworms.

The effect of the insecticide anthio on the densities of various microorganisms in the soil is rather different and depends on the amount of insecticide and the duration of its action. The insecticide anthio produces the succession in the species of microscopic fungi in associations already formed. A positive effect of this insecticide was noted on some fungal species of the genus Penicillium (P. godlewskii, P. canescens, P.mirczynskii). But due to the effect of anthio, some other species of fungi lose their ability to form organs of reproduction. Therefore an increase in the amount of sterile mycelium in the soil is noted.

Earthworms and their metabolites had a positive effect on the densities of microorganisms and stimulated the development of the fungi Mucorales. Due to these invertebrates the representatives of the genera Mortierella, Mucor, Absidia, Rhizopus have become more abundant.

The activity of fungi of the genus Trichoderma is intensified in the soil fertilized by straw.

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GROWTH OF BASIDIOMYCETES IN THE PRESENCE OF AGROCHEMICALS

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INTRODUCTION

The role of members of the Basidiomycetes in decomposition processes has been studied by relatively few researchers. The ability of many soil Basidiomycetes to break down lignin, noted by Falck (1923, 1930), is common in many wood-destroyers. On the other hand, Melin (1925) remarked that the mycorrhiza forming Basidiomycetes are incapable of utilizing cellulose or lignin but depend for their nutrition on carbohydrates derived from their host trees. It was subsequently shown by Norkrans (1950) that even some of the mycorrhizal fungi are capable of decomposing at least cellulose.

Lindeberg (1944, 1946, 1948) studied the ability of soil inhabiting Basidiomycetes to decompose litter and its main constituents, cellulose and lignin. In addition, Norkrans (1944, 1950), Mikola (1954a) and Fries (1955) indicated that the ability to decompose these constituents is very common among soil fungi. The most active litter decomposers have been found among the genera of Marasmius, Mycena, Clitocybe, Collybia, Clavaria and Stropharia, and many wood destroying fungi found on decaying trees have decomposed litter effectively in vitro: Armillaria mellea and species of Flammula, Hypholoma, Pholiota and Polyporus (Lindeberg, 1946; Mikola, 1954a).

Thus the Basidiomycetes in soil represent a physiologically heterogeneous group and in order to determine their role in the soil, thorough investigations into the physiology of individual species are needed. The course of litter decomposition, including its speed and intermediate and final products, depends on three main factors: i) the physical and chemical properties of the litter, ii) the environmental conditions and iii) the organisms themselves. The factors in turn are interdependent. The significance of each individual factor in the decomposition of litter or wood is a matter for investigation. In addition, with the rapid escalation in biocide usage in agricultural and forestry practice, it is urgent that we evaluate the pressures which these compounds exert on the fungi responsible for decomposition processes. Biocides are considered to be indispensable aids in agricultural, horticultural and forestry practices, and a vast array of chemicals are applied directly to soil. Other agrochemicals enter the soil as run-off from treated aerial systems, or from drifting sprays.

During the course of studies on soil fungi, members of the Basidiomycetes have often been overlooked because of difficulties of isolation and identification. Chesters (1949) referred to "the secret of the higher Basidiomycetes": Warcup (1959), with his hyphal isolation technique, showed that Basidiomycetes can be recovered from the soil, and Warcup and Talbot (1962) were able to identify several species. However, these isolated studies give only a small indication of the work still to be done: other approaches, such as the cultivation of mycelia from sporophores, enable cultural studies to be carried out.

In the present study, three non-mycorrhizal species (235M, *Coprinus comatus* and *Cyathus stercoreus*), two known mycorrhizal species (*Boletus variegatus* and *Paxillus involutus*), and *Phallus impudicus*, a species of uncertain status, have been used to investigate the basic physiology and the reaction of each to the presence of agrochemicals. In this way comparisons can be made of the abilities of the nutritionally different species under a range of environmental pressures.

MATERIALS AND METHODS

Species

The fungi used in this study include: two species isolated from sporophore tissue, *Coprinus comatus* growing on a grass lawn, and *Phallus impudicus* growing among mosses in deciduous woodland; an unidentified Basidiomycete isolated from leaf litter of *Agrostis tenuis*, designated 235M; two known mycorrhizal species, *Boletus variegatus* and *Paxillus involutus* (supplied by Dr.P.Mason, Institute of Terrestrial Ecology, Edinburgh) and the non-mycorrhizal fungus *Cyathus stercoreus* (supplied by Dr. P. Blakeman, Aberdeen).

Media

All species were maintained on a modified Hagem malt agar (HMA) (Modess 1941) and contained per litre of distilled water: Glucose, 10g; NH_4Cl, 0.5g; $MgSO_4.7H_2O$, 0.5g; malt extract agar 50g; Fe Cl_3(1% solution), 10 drops.

The basic liquid medium (BLM) contained per litre of distilled water: Glucose, 10g; NH_4Cl, 0.5g; $MgSO_4.7H_2O$, 0.5g; KH_2PO_4, 0.5g; malt extract 20g; Thiamin, 1 mg; microelements (after Lilly and Barnett, 1953), 2ml.

Inocula for liquid cultures were cut from the growing edge of petri plate cultures on HMA. These inocula were transferred to the flasks and floated on the surface of the culture medium. All flasks were incubated as standing cultures.

Chemicals

Herbicides: Maxide 36 (as maleic hydrazide) - active ingredient (a.i.) 36% (w/v) 1,2-dihydro-3,6-pyridazynedione

Paraquat - a.i. 25% (w/v) 1,1'-dimethyl-4,4'-bipyridinium.

Fungicide: Verdasan - a.i. 2.5% (w/w) phenyl mercury acetate.

The field application rates of the agrochemicals are as follows:

Mazide:	approx. 4000 ppm
Paraquat:	approx. 800 ppm
Verdasan:	approx. 20 to 80 ppm

Effect of temperature on growth rate

Petri plates containing about 20 cm^3 of HMA were inoculated with a 5 mm disc cut from the margin of colonies growing on HMA. Plates were incubated at 5°, 10°, 15°, 20°, 25°, 30° and 35° C. The colony diameters were taken as the mean of two diameters at right angles to each other. Five replicate plates for each temperature for every fungus were used. Extension growth rates were calculated during the log phase of growth.

Dry weight increase

Flasks containing 20 ml BLM were inoculated with the test fungi and incubated at their optimum temperatures. Three replicate flasks for each consecutive sample for each fungus were used. For dry weight analysis flasks were removed, the mycelia harvested and dried to constant weights.

Effect of agrochemicals on growth

Appropriate amounts of herbicide stocks were added to BLM to give final concentrations of 500, 1000, 2000, 3000, 4000 and 8000 ppm (a.i.) for Mazide, and 5, 10, 25, 50, 100 and 250 ppm (a.i. for Paraquat. Flasks were autoclaved for 15 min and 15 psi. Appropriate amounts of Verdasan stock solution were added to cooled sterile BLM to give final concentrations of 0.1, 0.25, 0.5, 0.75, 1.0 and 2.5 ppm (a.i.). BLM without agrochemical addition was used as control. Five replicate flasks for each concentration of agrochemical for every fungus were used, and dry weight analysis performed as above.

RESULTS

Effect of temperature on growth rate

The results are summarised in Figure 1 and indicate the optimum growth temperatures. All six species grew at 5°C, the lowest temperature used. Four of the species investigated showed growth between 20° and 25°C (Basidiomycete 235M, Coprinus comatus, Boletus variegatus and Phallus impudicus). Paxillus involutus showed a lower optimum temperature, around 20°C, while Cyathus stercoreus had its optimum near 30°C.

In general, the two mycorrhizal species (P.involutus and B.variegatus) and P.impudicus did not grow above 30°C, whereas the other three non-mycorrhizal species grew above this temperature.

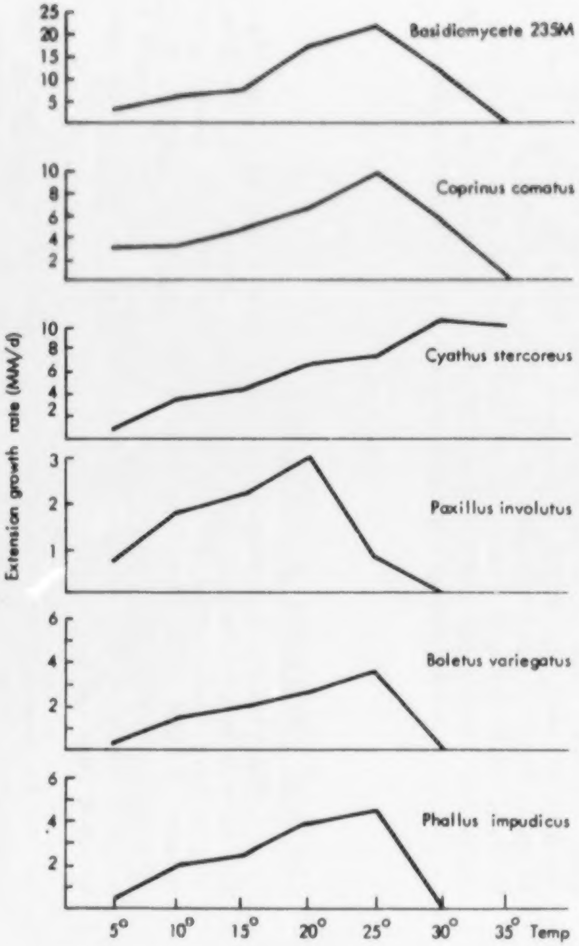

FIG 1. EFFECT OF TEMPERATURE ON MYCELIAL EXTENSION RATE OF SIX BASIDIOMYCETES ON HMA.

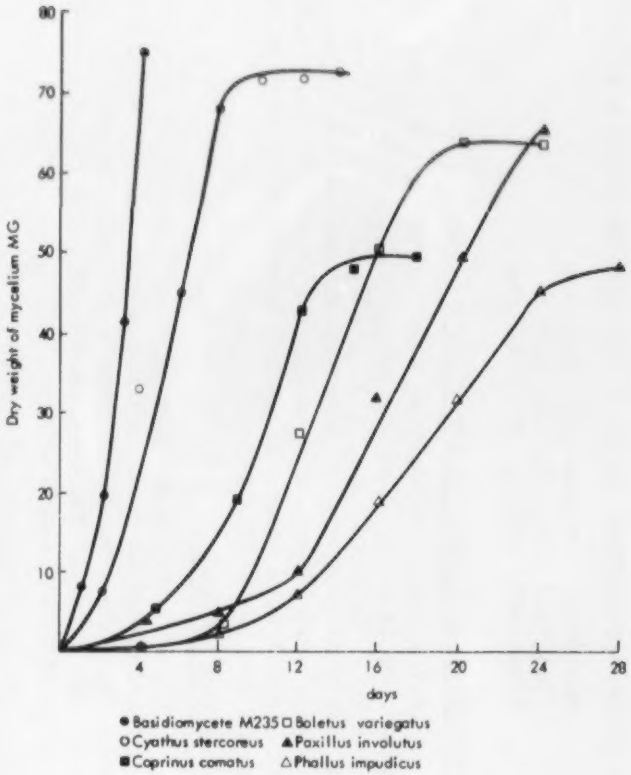

FIG 2. GROWTH OF SIX SPECIES IN LIQUID MEDIUM AT THEIR OPTIMUM TEMPERATURES

Dry weight increases

The three non-mycorrhizal species, 235M, C.comatus and C.stercoreus, showed relatively higher growth rates than did P.involutus, B.variegatus and P.impudicus (Table 1).

TABLE 1. Growth rate (mg dry weight/24 hr) of Basidiomycetes at their optimum temperature for growth.

Basidiomycetes 235M	33.50	Boletus variegatus	6.25
Cyathus stercoreus	9.38	Paxillus involutus	4.50
Coprinus comatus	7.67	Phallus impudicus	3.25

In addition, it is evident from Figure 2 that not only were growth rates slower in the two mycorrhizal species and P.impudicus but the lag phase of growth was, in general, considerably longer. Conversely, those species with a shorter lag phase also showed a faster growth rate.

Effect of agrochemicals on growth

The effects of the agrochemicals on the growth of the six Basidiomycetes are shown in Figures 3, 4 and 5. In general the fungi were relatively tolerant to Mazide at the concentrations used: only Phallus impudicus was inhibited at concentrations above 1000 ppm. Paraquat and Verdasan showed some similarities in their effects on growth at the concentrations used: 235M and Coprinus comatus were more tolerant than the other species. Boletus variegatus and Paxillus involutus were least tolerant, being inhibited at 5 ppm of Paraquat and 0.1 ppm of Verdasan. Cyathus stercoreus and Phallus impudicus showed growth patterns similar to the mycorrhizal species in the presence of Paraquat, but both were more tolerant than these species to Verdasan.

DISCUSSION

In earlier studies on Basidiomycetes, most have been found to be mesophilic in their temperature requirements. Three mycorrhizal species of Boletus studied by Melin (1925) showed optimum growth at 25°C, while Mikola (1948) found a slightly lower optimum for species of Amanita and Lactarius. Norkrans (1950) found that mycorrhizal Tricholoma species had optima within the range 18° to 30°C, while Marx (1969) showed that Pisolithus tinctorius grew best at 30 to 35°C. Laiho (1970) reported the temperature maximum for eight strains of Paxillus involutus to be about 30°C, with all strains being killed at 32°C.

Of the various wood-destroying Hymenomycetes studied by Humphrey and Siggers (1933) and Björkman (1946) belonging to the

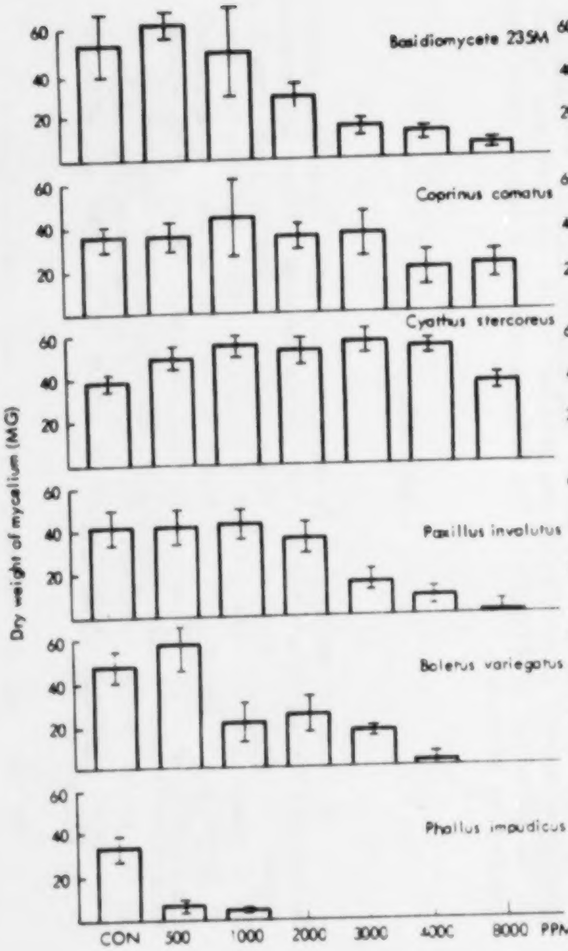

FIG 3. EFFECT OF MAZIDE ON GROWTH

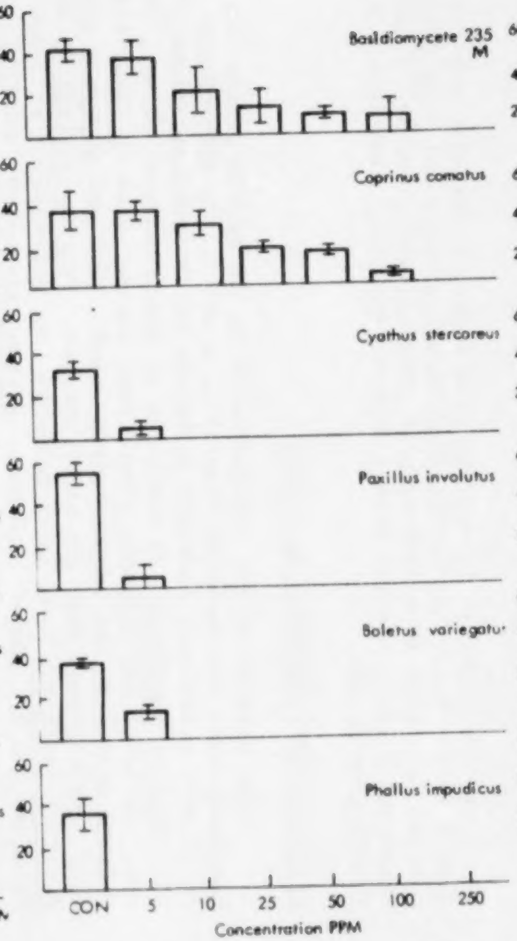

FIG 4. EFFECT OF PARAQUAT ON GROWTH

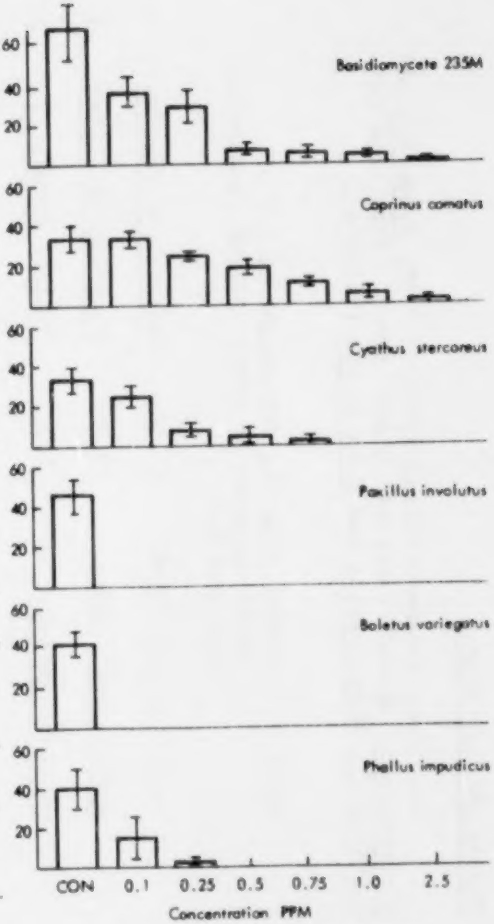

FIG 5. EFFECT OF VERDASAN ON GROWTH

genera *Polyporus*, *Stereum* and *Poria*, the great majority have maximum growth at temperatures of 28°C or higher. On the other hand, several *Mycena* species grew best at 20°C (N. Fries, 1949). Treschow (1944) found the coprophile *Psalliota bispora* to grow best at a temperature range between 20° and 27°C with the optimum at 24°C. The coprophilic species of *Coprinus* investigated by Rege (1927) showed a high optimum of 30° to 35° while L.Fries (1956) found various species to grow best at 30° to 35°C with good growth at 44°C in one species.

In the present study, the six species used were also mesophilic, with *Cyathus stercoreus* showing the highest temperature range. All six species exhibited growth at 5°C, and there were indications that *Coprinus comatus* could probably grow quite well at lower temperatures. Melin (1925) found that three species of *Boletus* grew well at 10°C and two of them continued to grow at 6°C, while Lobanow (1960) reported that the temperature minimum of mycorrhizal fungi was 1° to 5°C. However, temperature requirements can depend on the origin of the strains used: Moser (1958a) showed that the minimum for a strain of *P.involutus* isolated from a valley was 2° to 8°C, whereas a mountain strain grew at -2°C to 4°C.

Soil inhabiting Basidiomycetes have long been regarded as slow growing organisms. However, Basidiomycete 235M is exceptional in showing a rate of growth comparable with many non-Basidiomycetes. *Phallus impudicus* and the two mycorrhizal species tested were not only slower growing than the other non-mycorrhizal fungi, but they also showed a much longer lag phase. Further studies are in hand to see whether the growth rate can be used as a criterion for distinguishing between mycorrhizal and non-mycorrhizal fungi.

In the presence of the agrochemicals used, there were again some differences in the tolerance shown by the mycorrhizal and non-mycorrhizal species. With the exception of *Phallus impudicus* the mycorrhizal species were less tolerant than the non-mycorrhizal species to the three chemicals used. At field concentrations, all species except *Phallus impudicus* were tolerant to Mazide. With Paraquat and Verdasan, however, all of the test fungi were inhibited below the field application rate.

The behaviour of *Phallus impudicus* indicates many similarities with the known mycorrhizal *Boletus variegatus* and *Paxillus involutus*. However, Grainger (1962) described it as growing saprophytically on leaf mould and decayed wood, while Trappe (1962) reported it as a possible mycorrhizal species.

Thus, the use of these agrochemicals could have more deleterious effects on mycorrhizal activity than on decomposition in general. This could be particularly important in those marginal situations where higher plant growth is dependent on mycorrhizal associations.

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RELATION BETWEEN SPECIES LISTS AND TOLERANCE TO NEMATICIDES

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INTRODUCTION

One body of ecological theory asserts that the physiological properties of the individual organisms in a collection are related to the number of species in that collection. Slobodkin and Sanders (1969) have suggested the possibility that where there are many species in a community some degree of species packing (MacArthur and Levins, 1967) has occurred, and that each individual from a collection containing many species may be expected to be less tolerant of perturbation than each individual in a collection with smaller numbers of species involved. In this sense, a community comprising a large number of "tightly packed" species should be less stable than one consisting of a smaller number of "loosely packed" ones. Most investigators from their own experience can think of systems which seem to confirm (or, perhaps, deny) the previous sentence, but this involves selection of evidence and does not constitute a test.

We wanted data which constituted objective samples of clearly comparable communities, which were accessible to collection and perturbation, but which had not previously been subjected to extensive analysis from the standpoint of our hypothesis. We therefore chose to study nematodes.

Nematodes were chosen to test the hypothesis because they are an integral part of the soil fauna, and may be either harmful as parasites of plant roots or beneficial in decomposition processes. It is also of economic importance to know how nematode communities in the soil will be affected by a pesticide perturbation.

Our sampling procedure was one routinely used in soil nematology. From each location we had a list of organisms present and relative abundance data. For discussion of the significance of such lists see Botkin et al. 1979, Maguire et al. 1980.

The perturbation was the application of an agricultural nematicide to a sample of living organisms in the laboratory. Since the hypothesis relates to the properties of individuals, the perturbation need not be performed in nature. It might be argued that extraction itself is a perturbation which preselects for differential response to nematicides but this seems far fetched.

METHODS

In this study seven localities were identified; four of these could be considered species-rich in nematodes. These were all in the botanical garden at the University of California, Riverside. We considered these to be a sample of "tightly packed" nematode communities. The other three communities were normally stressed by dryness and we expected to find only a few species of nematodes. These were located in a native coastal sage scrub community on a nearby ecological area, also on the UCR campus. Soil samples were taken at the base of the plant (near) or at the plant canopy (far). The localities were: Botanical Gardens - (a) *Juglans pyriformis* near, (b) *J. pyriformis* far, (c) *J. hybrid* near, (d) *J. hybrid* far; Sage Scrub - (e) bare ground, (f) *Ambrosia dumosa* near, (g) *A. dumosa* far.

Soil samples were taken in the spring of 1977, the nematodes extracted, and the genera found in the first approximately one hundred individuals examined from each site were recorded. One hundred hand picked live nematodes from each site were placed into a solution of nematicide, 250 ppm 1,3 - dichloropropene. The time to 50% immobilization was determined. (Immobilization is used as a criterion of the effectiveness of a nematicide because the actual death point of a nematode is difficult to determine from visual observation). Solutions were examined for immobilized nematodes every 5-6 minutes and at the termination of the 5-minute interval after immobilization had exceeded 50%, a differential count was made of the first one hundred mobile animals encountered. This was repeated on separate samples, March 21 and March 22, 1977, so that two measures were made from each community. For statistical purposes they were treated as independent samples.

RESULTS

The list and number of nematode genera found in each sample before and after treatment are shown in Tables 1 and 2. As expected, the mean number of genera found in each sample from the Botanical Gardens were greater than those in the coastal sage scrub (10.4 vs. 5.5). A median test showed that more species were lost from the species-rich garden communities than from the species-poor scrub areas (4.9 vs. 3.0) ($X^2 = 7.87$, df = 2, $P < .05$). However, there were more genera there initially to lose; the proportions of the genera lost in the two areas (.39 vs. .27), while in the same direction, was not significantly different when tested with a median test ($\underline{\underline{X}}^2 = 1.17$, df = 3, $P > .7$).

It should be recognized that the number of species present is but one measure of community structure. Lewontin (1969) has stressed that community stability should be measured in a variety of ways. A way to do this is to compare the vectors of the species composition before and after treatment. Prior to treatment with nematicides each population can be represented by a vector $\underset{\sim}{P}_B = (P_1, P_2, \ldots . P_K), \Sigma P_i = 1$, where the components represent the proportion of each genus in making up the sample.

TABLE 1. Nematode genera present in soil samples before and after treatment with a nematicide.

	DAY 1													
Location	A		B		C		D		E		F		G	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
# species	13	6	11	6	12	7	11	6	5	5	7	4	7	5
Acrobeles	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Acrobeloides	+	+	+	+	+	+	+	+	+	+	+		+	+
Alaimus	+		+		+		+							
Diptherophora	+													
Ditylenchus			+		+						+		+	
Dorylaimus	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Meloidogyne	+													
Merlinius	+		+		+	+	+							
Monhystera														
Paraphelenchus	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Paratylenchus	+		+	+	+		+							
Pratylenchus									+	+	+	+	+	+
Prismatolaimus	+	+												
Psilenchus	+													
Quinsulcius					+									
Rhabditis	+	+	+	+	+	+	+	+						
Trichodorus			+				+							
Tylenchorhynchus											+	+	+	+
Tylenchus			+		+	+	+	+						
Xiphinema	+				+		+							

DAY 2

Location #	A		B		C		D		E		F		G	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
species	14	11	14	9	13	7	12	9	8	6	7	5	8	5
Acrobeles	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Acrobeloides	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Alaimus	+		+		+		+							
Aphelenchoides							+	+						
Cervidellus					+				+					
Diptherophora	+	+	+											
Ditylenchus					+								+	
Dorylaimus	+	+	+	+	+		+	+	+	+	+		+	+
Merlinius	+	+	+	+	+	+			+				+	+
Monhystera	+	+	+	+	+									
Paraphelenchus	+		+	+			+	+	+	+	+		+	
Paratylenchus	+	+	+	+	+	+	+	+						
Plectus	+	+	+	+	+	+	+	+	+	+	+	+		
Pratylenchus									+	+	+	+	+	+
Prismatolaimus	+	+	+											
Psilenchus			+											
Rhabditis	+	+	+	+	+	+	+	+						
Trichodorus							+							
Tylenchorhynchus											+	+		
Tylenchus	+		+		+		+	+					+	
Xiphinema	+	+			+	+	+							

Table 2

Number of nematode genera present in soil samples before and after treatment with a nematicide.

Number of Genera

Location Species-rich communities (Botanical Gardens)	Day 1				Day 2				Average Day 1/Day2	
	Before nematicide	After nematicide	Change	% Loss in genera	Before nematicide	After nematicide	Change	% Loss in genera	Ave change	Ave % loss
A	13	6	-7	-.54	14	11	-3	-.21	-5	-.37
B	11	6	-5	-.45	14	9	-5	-.36	-5	-.40
C	12	7	-5	-.42	13	7	-6	-.46	-5.5	-.44
D	11	6	-5	-.45	12	9	-3	-.25	-4	-.35
Ave	11.75	6.25	-5.5	-.465	13.25	9	-4.25	-.32	-4.87	-.39
Species-poor (Sage Scrub)										
E	5	5	0	0	8	6	-2	-.25	-1	-.12
F	7	4	-3	-.43	7	5	-2	-.29	-2.5	-.36
G	7	5	-2	-.29	8	5	-3	-.38	-2.5	-.34
Ave	5.66	4.66	-1.66	-.24	7.66	5.33	-2.33	-.31	-3.0	-.27

After treatment, the communities would be changed to a new vector of compositions ($\underset{\sim}{P}_A$). (We have used proportionate abundance because absolute species abundance could not be estimated).

Community stability can be measured in a number of ways. We chose to measure Euclidean distance between the position vectors before and after treatment. A more stable community should be moved less. We also determined the angle between the vectors $\underset{\sim}{P}_A$ and $\underset{\sim}{P}_B$. A more stable community should be moved through a smaller angle by the nematicide. The Euclidean distance in n-space, where n is the number of genera prior to treatment, and the angle between community vectors before and after treatment are compared (Table 3).

There was a greater effect on the more species-rich communities. The nematicide moved the species-rich communities an average distance of .90 genera, whereas the species-poor communities were moved a distance of only .57 genera. This difference was significant by a Mann-Whitney U-test ($U=6$, $P<.01$). The angles through which the communities were moved also differed significantly ($U=7.5$, $P<.05$) with the species-rich communities being again more affected.

These data suggest that species-packing is an important determinant of community stability. It suggests also that the mathematical theories of community stability may be helpful for better understanding the effects of pesticides on plant and animal communities.

Table 3

Stability of species-rich and species-poor nematode communities. Stability is measured by the resistance to change in species composition vectors by treatment with a nematicide.

Location	Euclidean distance between vectors before and after nematicide			Differences in angles between vectors before and after nematicide		
Botanical Gardens	Day 1	Day 2	Ave.	Day 1	Day 2	Ave.
A	0.87	0.63	0.75	30	37	33.5
B	0.88	1.29	1.1	52	80	66
C	0.74	1.01	0.87	43	61	52
D	0.74	1.04	0.90	43	63	53
Ave	0.80	0.99	0.90	35.25	60.25	51.12
Sage Scrub						
E	0.46	0.66	0.56	26	39	32.5
F	0.52	0.35	0.44	30	20	25.0
G	0.96	0.45	0.70	57	26	41.5
Ave	0.65	0.49	0.57	37.7	28.3	33.0

DISCUSSION

There has developed an extensive and polemical literature on the relation between species packing and environmental stability. Much discussion has focussed on whether or nor particular environments ought to be thought of as more or less stable and on various definitions of stability. In addition there has been concern as to statistical problems in the determination of diversity. These problems remain unresolved. Obviously the stability of the environment must be viewed from the standpoint of particular organisms. What constitutes perturbation in one kind of organism will not in any way disturb another. Also most measures of species diversity are subject to various interpretations.

The Slobodkin-Sanders (1969) formulation of the role of stability in contributing to diversity asserts that there exists a relation between the number of species and the physiological properties of the individual organisms in collections of organisms made in nature. This connection is not obvious. It might, for example, be asserted that if one kind of organism in a particular place is particularly sensitive to some environmental event then others in the same place might share that sensitivity but this assertion would say nothing about the number of species to be expected in that place. Perhaps the most significant aspect of the Slobodkin-Sanders formulation is that it attempts to explicitly rationalize a connection between physiological properties of individual organisms and properties of assemblages of species in which they are found. Testing detailed aspects of the Slobodkin-Sanders theory would require an enormous amount of time and effort in studying several ecosystems. In the absence of general agreement on clear definitions of stability and ambiguity as to the relative merits of different diversity measures such tests would still be equivocal. We have not attempted this - rather we asked the simpler question - whether we can demonstrate any relation at all between the number of species in a collection and the physiological properties of the individual organisms. In the absence of such a relation any attempt at rationalization of species diversity in terms of biological properties is suspect.

We used an unnatural perturbation, the nematicide, to avoid the possibility that we are mimicking a natural event which the organisms might not find perturbing. Our choice of statistical procedure was dictated by our desire to use as much of the information in our data as possible, and to minimize the role of special distributional functions.

If we had studied a well understood community we would legitimately be subject to the criticism that we had chosen either the community or the perturbation because of prior knowledge of how the organisms would respond. Our choice of organisms was motivated by our desire to approach as closely as possible a blind test of the simple hypothesis that there was in fact a relation between length of species lists and physiological properties.

The fact that we did show that the longer species-list samples were more sensitive than the shorter does not by any means demonstrate universal validity for the Slobodkin-Sanders argument. It does demonstrate a specific prediction of the formulation; using our criteria for diversity and for statistical difference, the hypothesis was confirmed. This of itself is of significance in light of the assertion by Abele and Walters (1979) that the hypothesis is a tautology, i.e. is untestable.

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A PRELIMINARY STUDY OF THE USE OF SOME SOIL MITES IN BIOASSAYS FOR PESTICIDE RESIDUE DETECTION

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INTRODUCTION

Our objective in this paper is to analyze the methodology of bioassays principally in relation to the detection of toxic residues of pesticides through soil fauna. In this sense, our conception is in accord with that of Ruzicka (1973): "The determination of pesticide residues by bioassays is based on the measurement of growth, death or some other physiological (or ecological) change in animals, plants or microorganisms." The concept of bioassay derives from that of the bioindicator. A bioindicator is in all biological parameters, qualitative or quantitative (measured at individual, population or community level) likely to indicate the particular life conditions corresponding either to a given state, to a natural variation or to an environmental perturbation. Thus, in the sense of the naturalists, this definition includes the more restrictive terms of indicator or characteristic species. The actual revival of these old concepts comes especially from actual needs concerning ecological evaluation, quantification of their biological value and ecosystem quality. In this context, and by referring to soil ecosystem, the problem of bioassays becomes more and more essential for soil biology and necessitates certain adjustments. On the other hand, as of now a distinction should be made between bioassay and screening. Screening is based principally on the comparison of direct mortality induced by various molecules on whatever species, either noxious or non-target. On the contrary, by definition, bioassay refers to standard organisms taken as a measure of reference. In addition, we do not foresee the direct repercussion of pesticides in the field or the consequence of their use on soil organisms. These aspects, which constitute a global approach and not strict bioassays, have been synthesized by several authors throughout the past few years (Edwards, 1973a, b; Thompson and Edwards, 1974; Matsumura, 1975; Brown, 1977).

OBJECTIVE OF BIOASSAY TECHNIQUE

The objectives of bioassays, in the restricted sense of the term, can be classified into four categories:

1. The study of the persistance in function of the behavior of pesticides such as mobility and influence of external factors on the biocactivity.

2. The comparison of molecular analogues in the perspective of proposing a compatible choice with ecological imperatives in the sense of minimizing destructive effects on environment.

3. Demonstration of secondary effects;

    a. the induction of resistance,
    b. demecological (population level) such as influence on the fecundity of non-target species, or biocenotical modifications such as biomagnification, and
    c. the indication of teratologic effects.

4. The detection and measure of biological residual activity of pesticides;

    a. either with laboratory experiments (absolute bioactivity), or
    b. from field samples (relative bioactivity).

We are essentially developing the latter objectives, but we can briefly give a few samples concerning others in the context of soil biology.

RESEARCH REVIEW

Behavior of Pesticides

As Lichtenstein (1966) and Edwards (1973b) recalled, the bioactivity of soil pesticides depends on a number of factors, such as the chemical characteristics of the molecule, the type of treatment, the type of soil, the organic matter content, clay content, acidity, the temperature and water content of the soil, the type of vegetation or crop. Interesting studies carried out by Read (1969, 1971, 1976) by Harris (1969, 1972, 1973) by Harris and Sans (1972) by Griffiths and Smith (1973) on crickets, flies and cutworms have pointed out the importance of these factors on the real biological activity of insecticides. Among soil fauna, some species of collemboles, especially Folsomia candida, have been studied within this view, mainly by Thompson and Gore (1972), Thompson (1973) and by Tomlin (1975, 1977a, b). Here are two examples of these studies. The first (Table 1) shows that the bioactivity, and thus the hazardous effects of pesticides, can vary considerably depending upon the species. In the second example (Table 2) it is the type of soil and particularly the organic matter content which proves to be a criterion equally determinant. This is already proof of the superiority of biological analysis versus chemical analysis since for equivalent concentrations of pesticides the effects expressed in total bioactivity vary in very large proportions. In both cases, the chemical analysis would have lead to a simple equivalence of activity.

Table 1. Comparative Bioactivity of Some Insecticides on 2 Collembolan species (after Tomlin, 1975)

Insecticide		Bioactivity (% mortality)	
		Onychiurus justi porteri	Folsomia candida
Counter.$^{(R)}$ at:	0.05 ppm	9%	100%
	0.1 ppm	73%	100%
	0.5 ppm	96%	100%
Carbofuran at:	0.5 ppm	0%	15%
	0.1 ppm	0%	100%
	0.5 ppm	0%	100%
	1.0 ppm	35%	100%

Table 2. Influence of Soil Type on the Bioactivity of Technical Chlordane (Target: Crickets) (after Harris, 1972)

Soil Type	% Organic Matter	CL 50 (ppm)
Sand	0.5	0.46
Clay	27.8	6.56
Muck	64.6	18.82

Comparison of Pesticides

The comparison of the effects of analogues pesticides is one of the most positive aspects of bioassays because soil ecologists can recommend or impose the least prejudicial molecules in the edaphic environment (Table 3). The three pesticides mentioned are, in principle, equivalent as to their capacity of crop protection. This comparison recommends not

Table 3. Bioactivity of some Carbamate Insecticides on *Lumbricus herculeus* (from Lebrun and Klein, in pre.)

	CL 50 (5 hours of immersion)	Toxicity Ratio
Aldicarbe	2.9 ppm	1 : 1
Carbofuran	10.6 ppm	3.6 : 1
Thiphanox	26.8 ppm	9.2 : 1

only to make a choice as to the less harmful compound, but also it encourages studies directed at selecting pesticides less and less toxic for the faunal decomposers. In this aspect, the study by Tomlin (1977b) is very interesting (see Table 4). It is obvious, indeed, that the first benomyl is more compatible with ecological demand than the other, and with benomyl itself.

Table 4. Toxicity (mortality %) of Soil Application of Benomyl and two Analogues to three species of Springtails

	Benomyl		Analogue 1 N-methylcarba-moyl-benzimidazole		Analogue 2 N-methylcarba-moyl-imidazole	
Concentration in Soil	5 ppm	10 ppm	5 ppm	10 ppm	5 ppm	10 ppm
Species						
Onychiurus justi porteri	40	100	0	0	0	100
Hypogastrura armata	40	100	0	0	0	100
Folsomia candida	100	100	0	0	0	100

Demonstration of Secondary Effects

Soil ecologists are quite concerned about the secondary effects of pesticides due to the very slight mobility and the very long persistance of pesticides in the daphic environment if compared, for example, with aquatic environment (Thompson and Edwards, 1974). Contrary to the studies on noxious insects (Read, 1965; Rajak et al., 1973), few works have been dedicated to resistance and modification of fecundity induced in soil microarthropods. As an example of demecological effect, one can mention the work of Gregoire-Wibo (1978), conducted with Folsomia candida, which showed that the selective pressure induced by carbofuran affects the fecundity already after three generations of the species. As far as the biocenotical aspects are concerned, numerous studies have been realized directly in the field to study prey/predator relationships (for example Sheals, 1956) or modifications of the community structure. These works extend beyond the frame of this presentation and cannot, by their nature, be considered as real bioassays. On the other hand, from an ecological point of view, the work conducted by Popp (1970) on the oribatid Hermannia convexa is a model study. Popp combined laboratory and field experiences in order to consider all the problems of contamination and the transfer of pesticides. In this manner Popp (1970) showed that mite dejections treated with reduced doses of dieldrin were extremely toxic (their bioactivity was tested on Daphna) and could be the beginning of an important contamination of decomposer trophic chains of the soil.

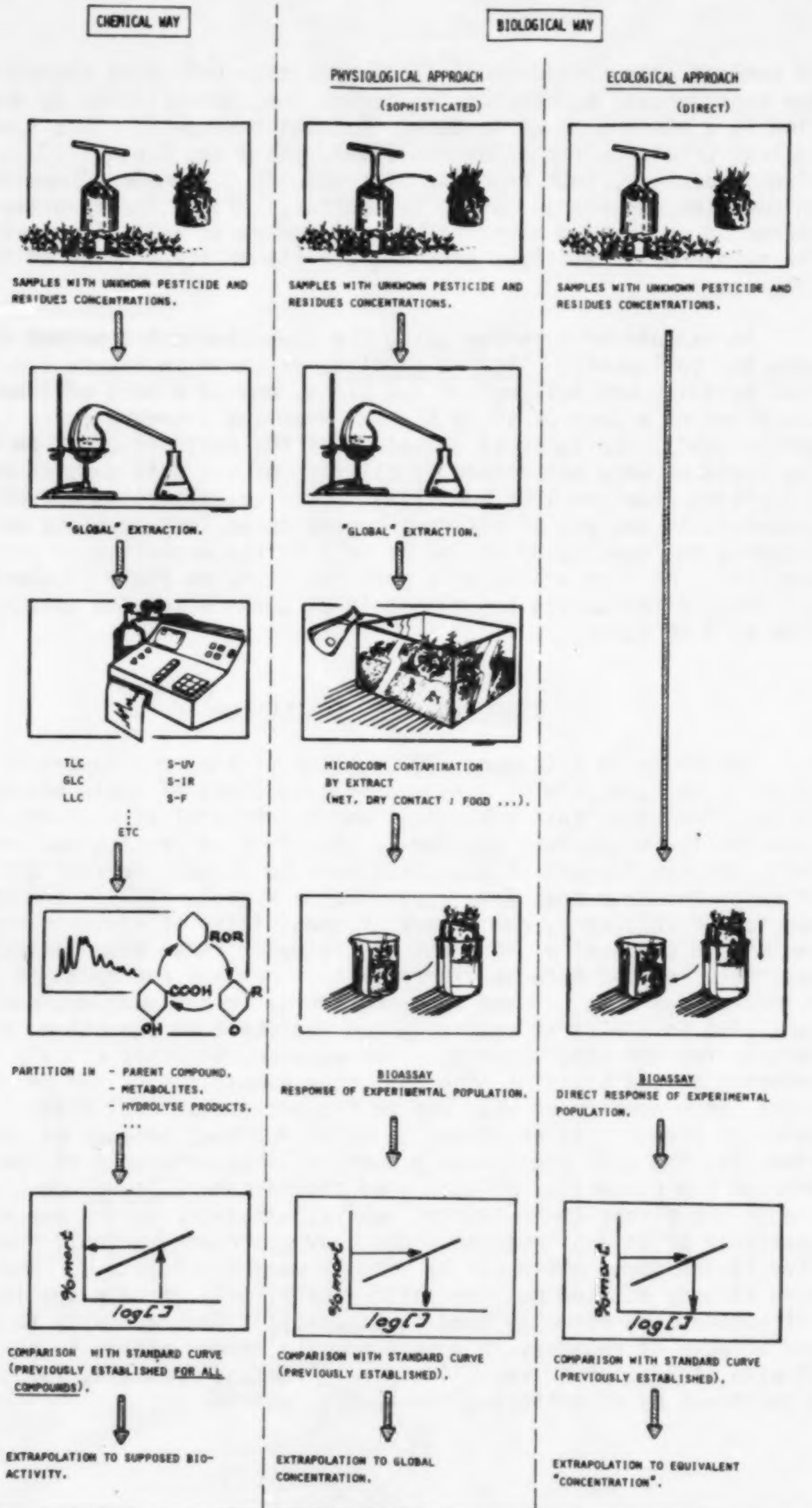
A PROPOSED RESEARCH DIRECTION

Detection and Measure of the Residual Bioactivity

Let us now approach the bioassay concept in the more restricted sense. The general scheme presented in Figure 1 illustrates the different methodological steps and compares the two possible approaches of bioassays (the physiological and ecological approach) with usual chemical approach. In all three cases, the problem remains the same, that is the detection and the quantification of residues and their possible activity on the tested fauna. Chemical analysis will certainly provide the most complete answer depending upon the techniques used such as spectrophotometry (S-UV, S-IR, S-F) and chromatography (TLC, GLC, LLC). One will obtain the exact spectrum of the parent compound, of its metabolites and of the hydrolized products. This information, however, as complete as it may be, does not clarify anything as far as the biological influence of the various toxicants. In fact, the knowledge of effects due to all combinations of concentrations between parent compound, metabolites, and hydrolized products would be necessary to provide the real value of the bioactivity. Besides, the variability of measures, as well as the difficulty in establishing techniques, make it so that the chemical analyses are restricted to very punctual problems.

Concerning biological assays, the information obtained is reversed as it is the bioactivity on which the attention is focused and not the chemical composition of the residues. However, the physiological approach and the ecological approach do not provide the same information. Only the ecological approach provides the actual toxicity of samples of the soil which are tested. As it appears in the figure, this technique gives a very rapid diagnosis that is often very precise as to the quality of the environment. After having established the tolerance of a sensitive species to one or another toxicant, we then put experimental populations

Fig. 1: COMPARISON OF METHOLOGICAL STEPS AND APPROACHES TO BIOASSAYS.


CHEMICAL WAY
SAMPLES WITH UNKNOWN PESTICIDE AND RESIDUES CONCENTRATIONS.
"GLOBAL" EXTRACTION.
TLC
GLC
LLC
S-UV
S-IR
S-F
ETC
ROR
COOH
R
OH
O
PARTITION IN - PARENT COMPOUND.
- METABOLITES.
- HYDROLYSE PRODUCTS.
...
%mort
log[ ]
COMPARISON WITH STANDARD CURVE (PREVIOUSLY ESTABLISHED FOR ALL COMPOUNDS).
EXTRAPOLATION TO SUPPOSED BIO-ACTIVITY.
BIOLOGICAL WAY
PHYSIOLOGICAL APPROACH
(SOPHISTICATED)
SAMPLES WITH UNKNOWN PESTICIDE AND RESIDUES CONCENTRATIONS.
"GLOBAL" EXTRACTION.
MICROCOSM CONTAMINATION BY EXTRACT (WET, DRY CONTACT ; FOOD ...).
BIOASSAY
RESPONSE OF EXPERIMENTAL POPULATION.
%mort
log[ ]
COMPARISON WITH STANDARD CURVE (PREVIOUSLY ESTABLISHED).
EXTRAPOLATION TO GLOBAL CONCENTRATION.
ECOLOGICAL APPROACH
(DIRECT)
SAMPLES WITH UNKNOWN PESTICIDE AND RESIDUES CONCENTRATIONS.
BIOASSAY
DIRECT RESPONSE OF EXPERIMENTAL POPULATION.
%mort
log[ ]
COMPARISON WITH STANDARD CURVE (PREVIOUSLY ESTABLISHED).
EXTRAPOLATION TO EQUIVALENT "CONCENTRATION".

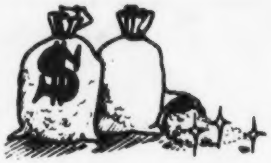
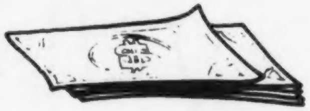
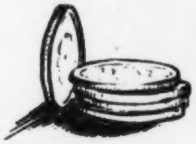
in contact with tested pedological samples. Following the mortality in the experimental population, we deduce the concentration by extrapolation in a given produce in terms of total toxicants. This type of biological trial, initiated by Sun (1957, 1963) and Gupta (1973), has already been put into practice with edaphic Collemoba (Thompson, 1973; Thirumurthi and Lebrun, 1977; Thirmurthi, 1979). The advantages of this method in comparison to others are presented in Table 5, which points out the number of repetitions possible and the relative price of the analysis.

An example of bioassay using the physiological approach was realized with the collembole, _Folsomia candida_, as given in Figure 2. The biological activity was followed in two plots, one at a dose of 2 kg AI/ha and the other at a dose of 10 kg AI/ha. With the standard curve (previously established), the temporal evolution of the residues could be observed. The residues were determined by dilution of the soil samples only for bioactivities reaching 100% mortality. This example shows one of the great interests in the use of microarthropods as an instrument to measure and diagnose the quality of soils, as well as the evolution of residual toxicity. As also proved by a parallel study on field populations, they can restore themselves approximately 24 weeks after the treatment at a dose of 2 kg AI/ha.

DISCUSSION AND CONCLUSIONS

According to Matsumura (1976), "One of the most important considerations in the analysis of residues is assessment of their potential damage. It is unfortunate that biological and biochemical assessment have not been really extensively applied to the field of residue analysis". In fact, the development of bioassays runs up against several difficulties of which the main ones are, according to Ruzicka (1973), the choice of species of reference, and a lack of specificity of living material in comparison to chemically different pesticides. These two difficulties are extremely related because discrimination between the residues of two molecules can only be done by using two different species, one being sensitive to the first pesticide and resistant to the other, and inversely for the other species. "In essence, bioassay animals are selected on the basis of high pesticide sensitivities and by the ease with which large numbers of them can be reared" (Matsumura, 1976). From this point of view, it is essential to point out that because of its great diversity the soil microfauna present a large reservoir of species presenting the properties of very good bioindicators (_sensu_ Jenkins, 1972). Due to the diversity in feeding habits, behavior, optima and ecological tolerance of soil microarthropods, they represent variable and sensitive living forms which can be largely used in bioassays. Now, as we have already pointed out for soil animals, only certain species of collemboles are actually used in bioassays. The necessity to measure the effects of residues in a more precise manner either in the soil (Tomlin, 1977a) or in vegetal tissue (Pree and Saunders, 1973) could be encountered by diversifying the living material.

TABLE 5 : COMPARATIVE ADVANTAGES OF CHEMICAL AND BIOLOGICAL WAYS.

	CHEMICAL WAY	**BIOLOGICAL WAY**	
		PHYSIOLOGICAL APPROACH	ECOLOGICAL APPROACH
KIND OF INFORMATION	-ABSOLUTE CHEMICAL COMPOSITION AND CONCENTRATION. -SUPPOSED BIOACTIVITY.	-ABSOLUTE (POTENTIAL) BIOACTIVITY. -GLOBAL CONCENTRATION.	-RELATIVE (ACTUAL) BIOACTIVITY. -EQUIVALENT CONCENTRATION.
COST			
TIME SPENT.	LONG	INTERMEDIATE	SHORT
NUMBER OF POSSIBLE REPLICATES	LITTLE	INTERMEDIATE	LARGE

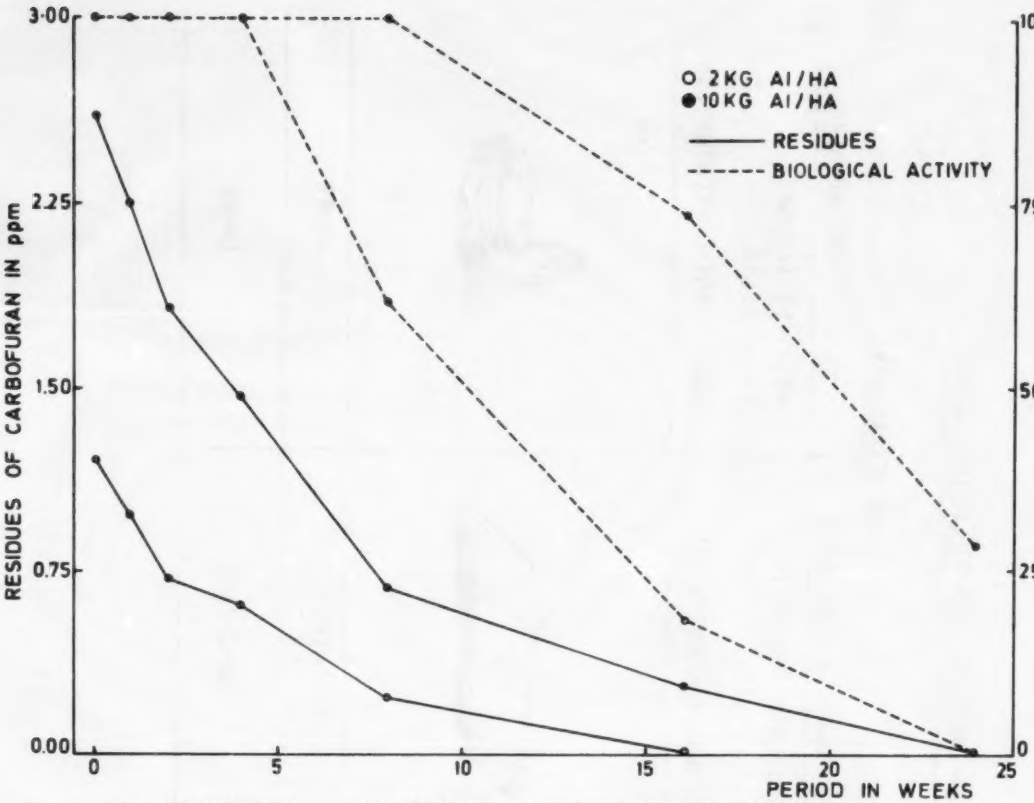


Fig. 2: ECO-TOXICOLOGICAL EVOLUTION OF CARBOFURAN RESIDUES TESTED *Folsomia candida* (After THIRUMURTHI and LEBRUN (1977)

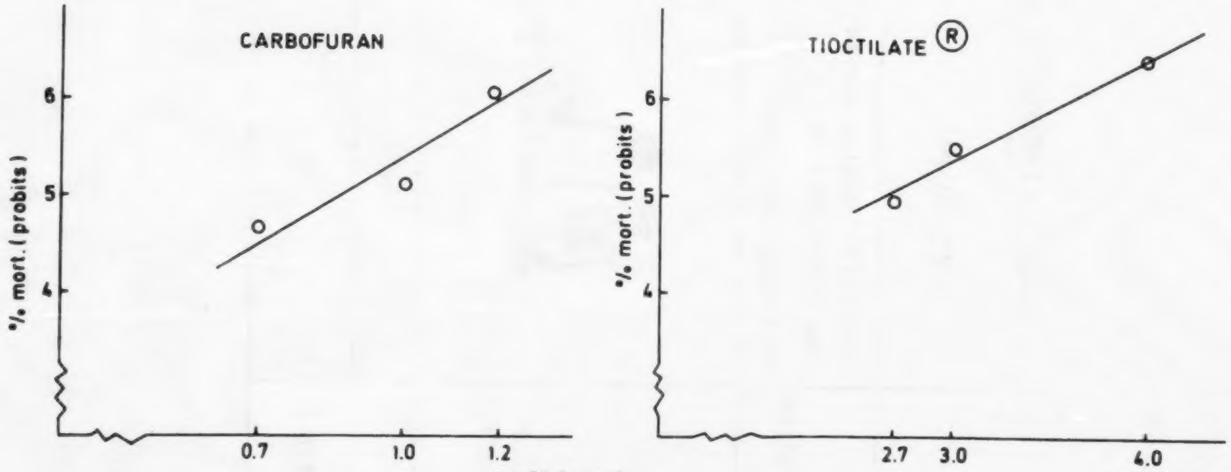


Fig. 3: TOXICITY OF ONE INSECTICIDE AND ONE MITICIDE ON PERGAMASUS NORVEGICUS (LARVAE) - (PRELIMINARY UNPUBLISHED RESULTS) - (MORTALITY AFTER 48 h)

Some preliminary tests have been performed in this sense on Oribatidei of the genus Damaeus (onustus and clavipes) (mycophagous species) and on gamasids of the species Pergamasus norvegicus (predatory species). The initial resulted obtained (Figure 3) show that with carbofuran the range of sensitivity is already very good, without attaining the range of 0.1 to 1 ppm, such as is generally recommended (Sun, 1957). On the other hand, the resistance of Pergamasus norvegicus to an acaricide, which is very active on tetranychids and oribatids, seems to invalidate the usually formulated criticism of non-specificity of biological material.

In conclusion we can only stress the development of bioassay methodology by using soil fauna. Table 6 summarizes the characteristics and qualities which should be sought after in the future for the species test, as well as for the diversification and the adjustment of an instrument for precise and reliable measures. In this view one must point out that the qualities of chosen species shall be encountered in the highest specialized species of which one different stasis will be selected. As far as the quality of assays, one must still stress the determination of the actual bioactivity which can only be estimated through an ecological approach. Finally, one must stress that what could be the most important is the need to continually control the biological quality and thus the maintenance of soil fertility.

TABLE 6. Use of microarthropods in bioassays - trends for the future

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QUALITIES OF THE TESTED - SPECIES

- High sensitivity
- Specificity to one (or a few number) pesticide
- Use of wild population (from untreated fields as forests)
- Reaction homogeneity (use of one stasis)
- Easy mass rearing and manipulation

QUALITIES OF THE MEASUREMENTS

- Simultaneous use of contrasting species (trophic levels, taxonomic status)
- Ecological approach (actual bioactivity)
- Need of continuous watch

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QUESTIONS and COMMENTS

H. EIJSACKERS: Don't you fear a change in genetical composition after mass rearing for a long time, so the species under study may not be representative anymore for the "wild" species selected at the start of the project?

Ph. LEBRUN: I agree with you but the laboratory strains could be characterized and isolated. On the other hand, for our strains, we regularly regenerate (in the genetical sense) the strains by adding some wild individuals directly coming from the field.

C.A. EDWARDS: Do you have any evidence for resistance developing when the same culture is exposed to a pesticide at intervals?

Ph. LEBRUN: Yes it is the case as Dr. Gregoire has shown on the *Folsomia candida* population treated with carbofuran at LC_{50}. After three generations the fecundity is increasing among intervals.

A.J. REINECKE: It is a well known fact that males and females of many species react differently in bio-assays. In some soil microarthropods sexual dimorphism develops at a fairly late stage which should be taken into account. Did you find the same persistent differences between the two sexes in their reaction to pesticides?

Ph. LEBRUN: In the case of Folsomia candida the problem is very simple as that species is a parthenogenetic one. The sexual discrimination is practically impossible on Oribatid mites. In the gamarid group, where the sexual differentiating is always possible, I observed no differences in reactions to pesticides.

However, in most cases, the sex is determined after the death of animals.

EFFECTS OF SIX BIOCIDES ON NON-TARGET SOIL MESOARTHROPODS FROM PASTURE ON STE. ROSALIE CLAY LOAM, ST. CLET, QUEBEC

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Canada

INTRODUCTION

Soil inhabiting insect pests have always been more difficult to control than their above ground counterparts. Some relief was achieved, however, with the introduction and use, often overuse, of DDT in the mid nineteen-forties and of cyclodiene biocides in the early nineteen-fifties (Harris et al. 1967). From that time onwards, synthetic organic biocides have impinged on both living and non-living parts of the environment (Figure 1) (Kevan, 1955; 1962; Rudd, 1964; Edwards, 1969; 1973; 1974; Gillett, 1970; Guyer, 1970; Mills and Alley, 1973; Butcher, 1976; Wallwork, 1976; McTaggart-Cowan, 1977; and Hill, 1978).

OBJECTIVES

Concern for possible detrimental effects of biocide use led to the establishment of a field trial to measure and suggest significance of changes in population densities of non-target soil mesoarthropod species, primarily Acari, in moderately intensively managed, cattle-grazed pasture on Ste. Rosalie clay-loam soil. The study site was on the farm of Mr. J. Martineau, St. Clet, Soulange Co., Quebec.

MATERIALS AND METHODS

The biocides[1] used for the present study were single, separately applied, operational dosages of diazinon, fenitrothion, malathion, methoxychlor, carbaryl and mexacarbate (Table 1). Experimental design was a linear random arrangement of pairs of like treatments having 0° magnetic azimuth and being perpendicular to prevailing winds.

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[1] Names of biocides are from Spencer (1973).

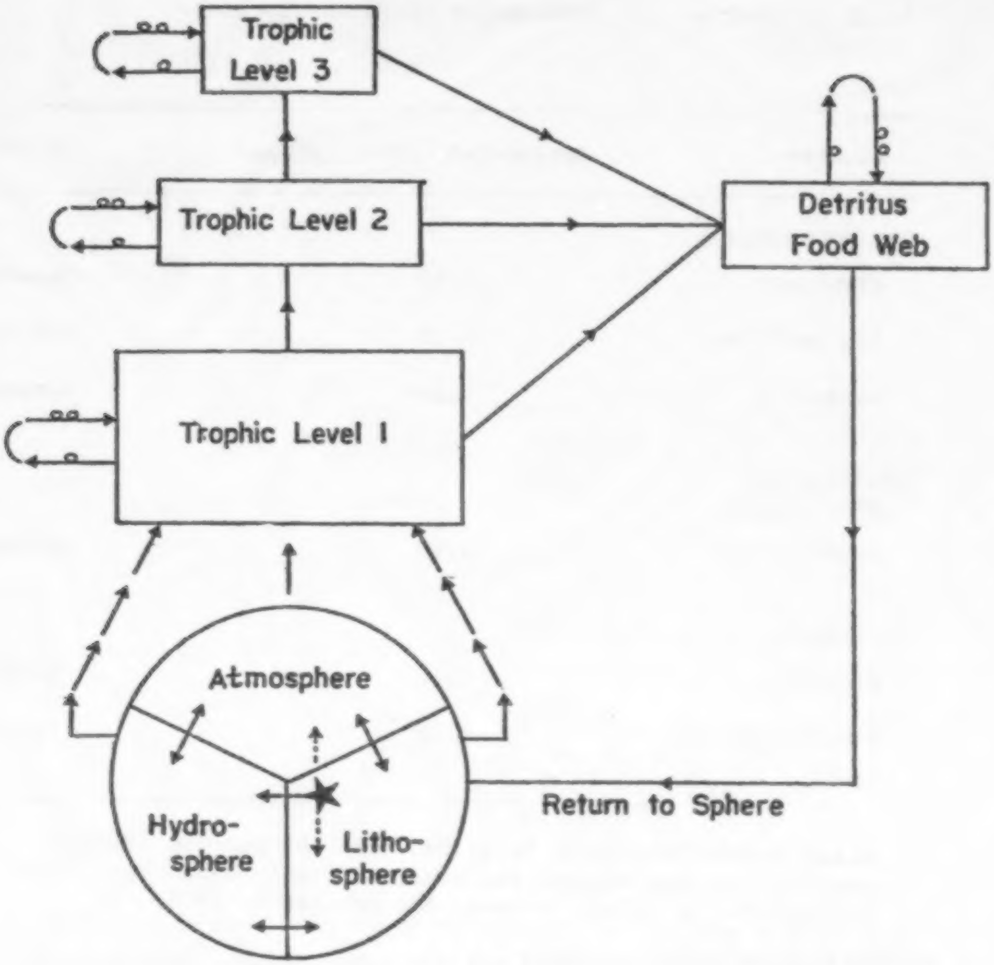
Trophic Level 3
Trophic Level 2
Trophic Level 1
Detritus Food Web
Atmosphere
Hydro-sphere
Litho-sphere
Return to Sphere

Figure 1: Scheme[1] of biocide transport within the biosphere.

★	Application of biocide to soil.
- - - - - -→	Direct movement of biocide into sphere from application source.
——→	Physical transport and degration of biocide.
—o→	Biological degradation of biocide.
—oo→	Return of modified biocide.

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[1] Modified from Robinson (1973).

TABLE 1: Sources and application rates of biocides.

Biocide	Application rate[1] (kg/ha)	Source
ORGANOPHOSPHATE		
diazinon	0.89	Commercial
fenitrothion	0.28	CIBA-GEIGY
malathion	0.20	Commercial
CHLORINATED HYDROCARBON		
methoxychlor	1.60	Commercial
CARBAMATE		
carbaryl	1.10	Commercial
mexacarbate	0.14	CIBA-GEIGY

[1] Based on manufacturer's label for best all purpose control; Fenitrothion and mexacarbate based on single application rate for control of spruce budworm, New Brunswick, 1969.

Insecticides were applied on 23 June, 1971, and samples collected on 21, 24 and 29 June, 6 and 20 July, and 17 August, 1971. Soil mesoarthropods were extracted in a modified Kempson, Lloyd and Gelardi (1963) infra-red extractor (Hill, 1969 and Behan, 1972).

ANALYSIS OF DATA

Since we were more interested in finding, than in not finding significant differences among population densities and dry-biomass values of soil mesoarthropod species from treated and control plots, we used a two-way analysis of variance and Duncan's Multiple Range Test (Duncan, 1955; Steel and Torrie, 1960; Chew, 1976a, b; 1977) (Tables 2 and 3).

Population densities and dry-biomass values were compared with those of pre-spray and/or control treatments (Figure 2).

TABLE 2. Analysis of data.

Group	Population Density	Dry Biomass
Total soil mesoarthropods	1	-
Zoophagous soil mesoarthropods	1	-
Phytophagous soil mesoarthropods	1	-
Zoophagous Acari	1	1
Phytophagous Acari	1	1
Acari[2]	1	1
"Other" soil mesoarthropods[2]	1	-

[1] Two-way analysis of variance and Duncan's Multiple Range test.

[2] Rarer taxa excluded.

- Data not determined.

CONCLUSIONS

1) Number of species, population densities and dry-biomass values of non-target soil mesoarthropods, were affected by the biocides used in this study, often in several ways.

2) Use of suprageneric groupings of soil mesoarthropods would have masked changes caused by biocides at the species or life-stage level.

3) Greatest reductions in population density and Acari dry-biomass normally occurred within two days after biocide application. Delayed reductions in population density and dry-biomass of phytophagous Acari occurred from one to two weeks after application of methoxychlor; and of population density of zoophages from one to four weeks after application of mexacarbate. A persistent reduction of zoophagous Acari dry-biomass occurred from 12 hours to two weeks after spraying mexacarbate.

TABLE 3a. Effects of biocides on soil mesoarthropod density and dry biomass according to Duncan's Multiple Range Test*.

POPULATION DENSITY	DRY BIOMASS
1) No significant difference among treatments:	
GROUP[1]	GROUP[1]
Phytophagous soil mesoarthropods[2]	Acari
	Zoophagous Acari
Hexapoda	
Entomobryidae[2]	Mesostigmata
Sminthuridae[2]	*Hypoaspis angusta*
Staphylinidae[2]	*Hypoaspis similisetae*
Diptera larva 1[2]	*Neojordensia levis*
Acari	Prostigmata
Zoophagous Acari	*Speleorchestes formicorum*
	Eupodes voxencollinus
Mesostigmata	
Macrocheles merdarius	Oribatei
	Brachychthorius jugatus
Prostigmata	
Speleorchestes formicorum	
Imparipes hystricinus	
Eupodes voxencollinus	
Coccorphagidia n.sp.	
Hauptmannia sp.	
Oribatei	
Immature Oribatei 1	
Immature Oribatei 2	
2) All biocide treatments significantly greater than control treatment:	
Collembola	Mesostigmata
Orychiuridae[2]	*Rhodacarellus silesiacus*
Mesostigmata	Oribatei
Rhodacarellus silesiacus	*Tectorepheus velatus*
Oribatei	*Oppia minus*
Tectocepheus velatus	
Oppia minus	
3) All biocide treatments significantly less than control treatment:	
Mesostigmata	Prostigmata
Trichouropoda obscura	*Bakerdania blumentritti*
Prostigmata	
Bakerdaria blumentritti	

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* Ste. Rosalie clay loam pasture, St. Clet, Quebec; Data for all sample dates from 21 June to 17 August, 1971.

TABLE 3b.

POPULATION DENSITY		DRY BIOMASS	
GROUP	Significant Biocide Treatment[3]	GROUP	Significant Biocide Treatment[3]
(4) Some biocide treatments significantly greater than control treatment:			
Hexapoda		Acari	
Eosentomidae[2]	dia., car.	Phytophagous Acari	dia., car., mex., mal., fen.
Aphidae[2]	car.		
Acari		Prostigmata	
Phytophagous Acari	car., dia.	*Tarsonemus randsi*	mex., car., dia., fen.
Prostigmata		*Coccorhagidia n.sp.*	met., mex.
Tarsonemus randsi	car., fen., mex., dia.		
Oribatei			
Brachychthonius jugatus	mal., car.		
Scheloribates pallidulus	car., mex.		
(5) Some biocide treatments significantly less than control treatment.			
Total soil mesoarthropods	dia., mex., mal., met., fen.	Mesostigmata	
		Trichoaropoda obscura	dia., fen., car., mex., met.
Hexapoda		*Macrocheles merdarius*	dia., mex.
Thripidae	mal., mel., mex., fen.	*Ololaelaps sellnicki*	met.
		Dendrolaelaps strenzkei	fen., mex., mal., met., car.
Mesostigmata		Prostigmata	
Hypoaspis angusta	dia., mex., car., mal., fen.	*Nanorchestes collinus*	met., mal., dia.
		Scutacarus lapponicus	dia., fen., mex.

TABLE 3b (Continued)

POPULATION DENSITY		DRY BIOMASS	
GROUP	Significant Biocide Treatment[3]	GROUP	Significant Biocide Treatment[3]
Hypoapis similisetae	fen., car., met., mal.	*Coccotydaelous krantzi* complex	dia.
Ololaelaps sellnicke	met.	*Stigmaeus sphagneti*	met.
Ameroscius corbiculus	met., mex., fen.	Oribatei	
Cheiroseius borealis	met., fen.	*Oppiella nova*	met., mal.
Asca bicornis complex	met., fen., mal., mex.		
Neojordensia levis	car., mal., mex., met.		
Dendrolaelaps strenzkei	fen., mal., met., mex., car.		
Pergamasus crassipes	car., fen., mex.		
Pergamasus lapponicus	car., met., fen., dia., mex.		
Prostigmata			
Stigmaeus sphagneti	dia., mex., met.		
Oribatei			
Oppiella nova	dia., met., mal.		
(6) Some biocide treatments significantly greater (>) or less (<) than control treatment:			
Hexapoda		Mesostigmata	
Hypogastruridae	>fen., dia. <met., mal.	*Ameroseius coribuculus*	>dia., car. <mex., fen.
		Cheiroseius borealis	>dia., car. <mex.
Prostigmata		*Asca bicornis* complex	>dia. <mex.
Nanorchestes collinus	>mex., car. <mal.		

TABLE 3b. (Continued)

POPULATION DENSITY		DRY BIOMASS	
GROUP	Significant Biocide Treatment[3]	GROUP	Significant Biocide Treatment[3]
Scutacarus lapponicus	<met. >dia., fen., mex.	*Pergamasus crassipes*	>mal, dia., met. <mex.
		Pergamasus lapponicus	>mal. <car., dia., mex.
Astigmata			
Tyrophagus dimidiatus	<car., dia. >met., mal., fen.	Prostigmata	
Rhizoglyphus rotundatus	<mex., dia, fen. >car, met.	*Hauptmannia* sp.	>mex. <mal.
Oribatei		Astigmata	
Trichogalumna n.sp.	>fen., dia., mex. <car., mal., met.	*Rhizoglyphus rotundatus*	>mex., fen., dia. <car., met.

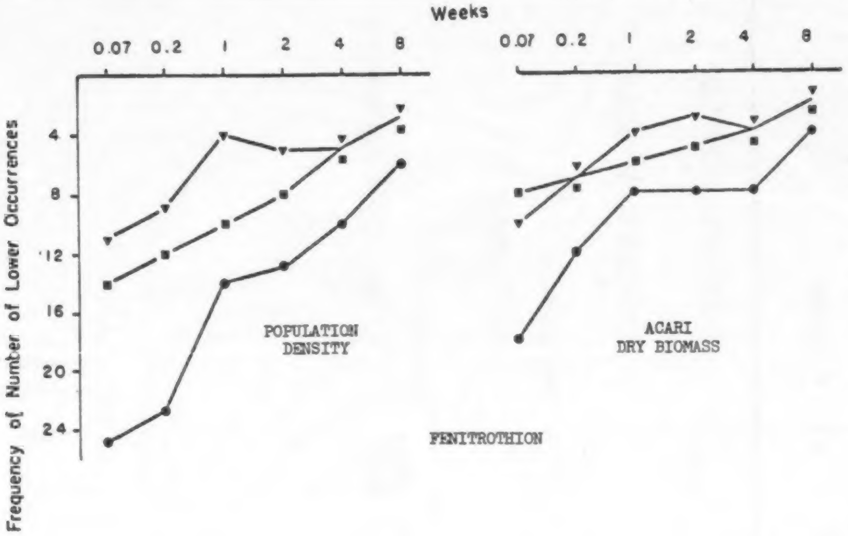
[1] Groups in phylogenetic order.

[2] Dry biomass values not determined.

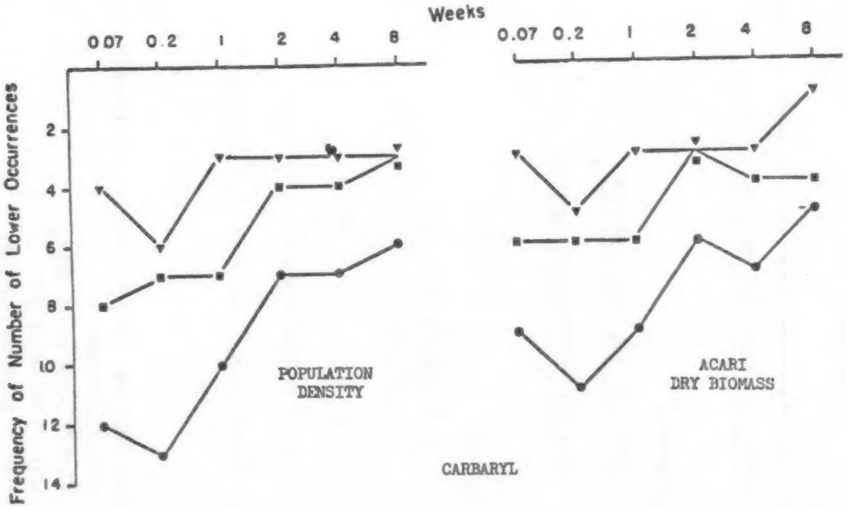
[3] Abbreviation for insecticide treatments:
dia = diazinon
fen = fenitrothion
mal = malathion
met = methoxychlor
car = carbaryl
mex = mexacarbate

FIGURE 3. Frequencies of number of occurrences when population density of soil mesoarthropods and dry biomass of soil Acari were lower than in controls, following biocide treatment. Ste. Rosalie clay loam pasture, St. Clet, P.Q. (23 June to 17 August, 1971).

●——● total soil mesoarthropods (population density)/Acari (dry biomass)
■——■ zoophagous " " " " "
▲——▲ phytophagous " " " " "

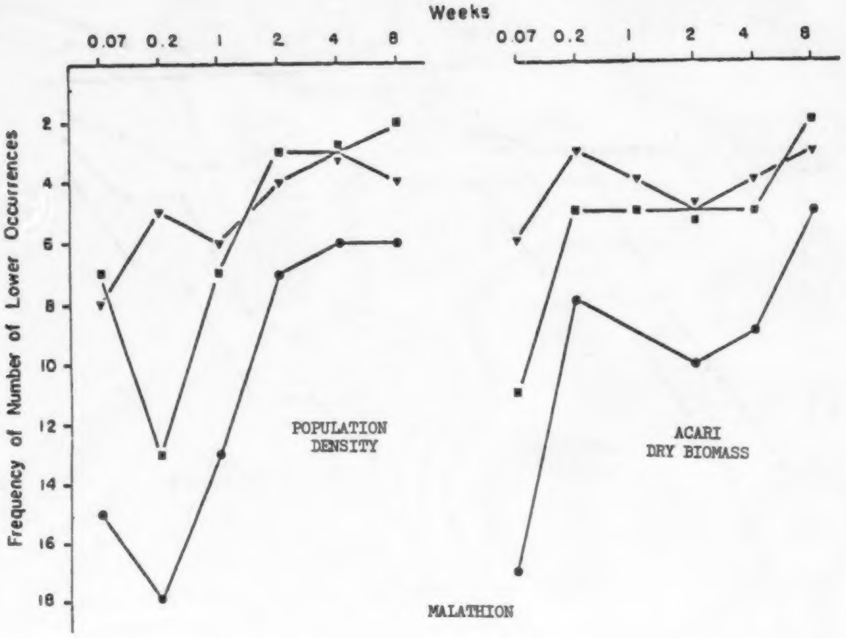


FENITROTHION



CARBARYL

FIGURE 3 (cont'd)



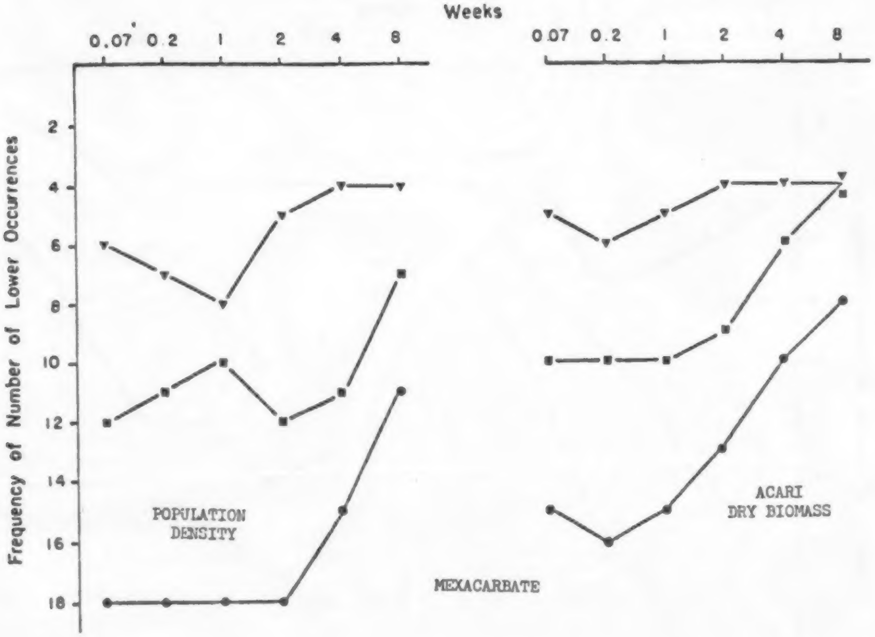
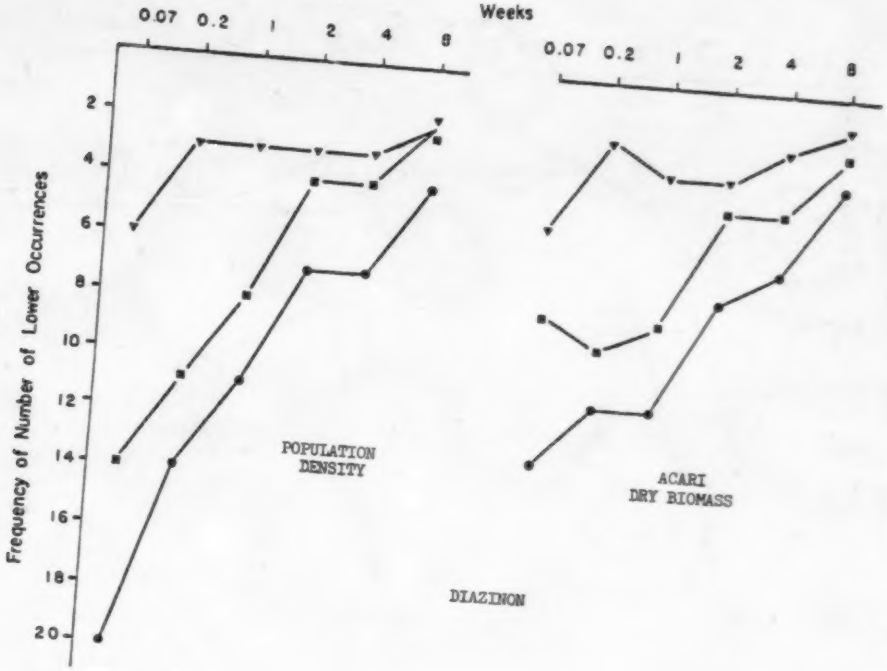
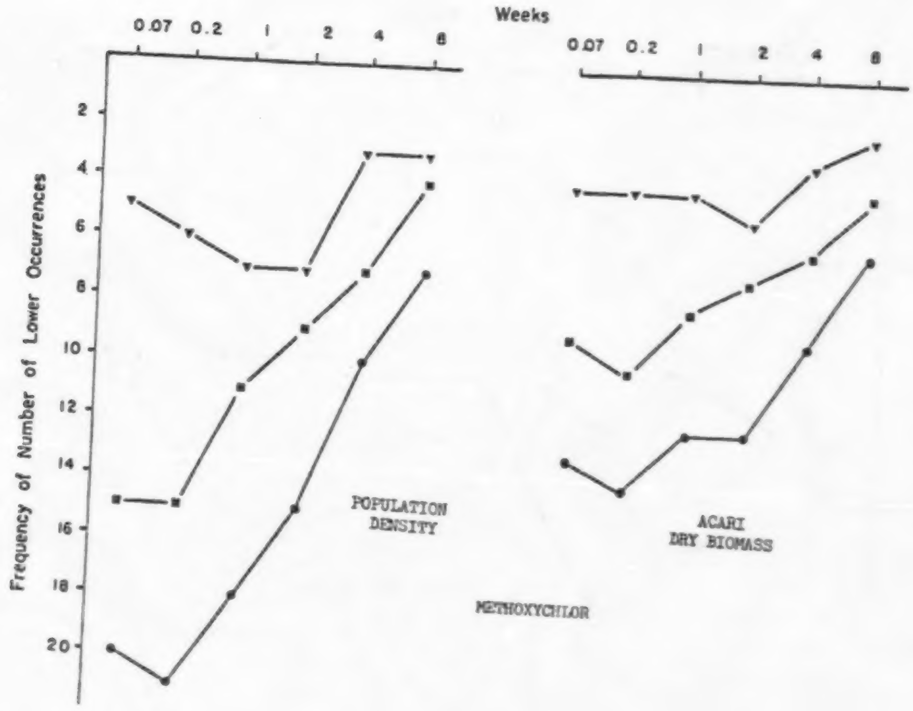


FIGURE 3 (cont'd)



DIAZINON



METHOXYCHLOR

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QUESTIONS and COMMENTS

G. BENGTSSON: Have you tried to analyze the mechanism of interaction between the different species used and the pesticides considering the different biological characteristics of the species and the chemical characteristics of the pesticides?

S.B. HILL: I have only examined this on paper in relation to various reviews of the literature that bear on this subject. My preliminary ideas have been published in the Proceedings of the Fourth North American Forest Soils Conference (Hill, S.B., L.J. Metz and M.H. Farrier, 1975. Soil mesofauna and Silvicultural Practices. Pages 119 to 135 in B. Benio and C.H. Winget (eds.) Forest Soils and Forest Land Management. Laval Univ. Press, Quebec) in relation to the mechanisms by which fertilizers might affect soil mesofauna in coniferous forest soils. Some of these are likely to be similar to the mechanisms involved in pesticide effects.

S.E-D.A. FAIZY: Please give the reason for the delay action of some insecticides on density of soil fauna and whether it is due to physiological reasons related to the fauna itself or due to a chemical and/or physical process going on in the soil.

S.B. HILL: I suspect that most delayed effects operate via the food chain and via (initially) sublethal effects that influence behavior and reproduction. Which of these is most important will vary from one species and one habitat to another.

K.H. DOMSCH: Do you know any confirmed field observations on reduced organic matter degradation following pesticide application at recommended rates?

S.B. HILL: No. I am, however, familiar with several farmers that I respect, who claim that such relationships exist at an economically significant level. There are, of course, various litter bag studies that have supported such conclusions. Dr. Satchell mentioned Dr. B.N.K. Davis' work on effects of pesticides on rate of organic matter decomposition. There was no significant difference and displaced millipedes were replaced by others. I believe that we should examine such short-term observations with caution as substitute species may have qualitatively different functions (e.g. that have a bearing on rate of release of certain trace minerals) whose effects may not become clear for 5, 10 or more years.

C.A. EDWARDS: I noted that you list *Rhodacarellus sileacus*, as a species that increases in number due to biocides. As this is a well-known predator, how do you explain these increases in numbers? Are they due to hyperpredation?

__S__.__B__. __HILL__: I do not know the answer. Certainly hyperpredation is one possibility. Reduced competition and invasion from adjacent areas or movement upwards from the profile below the emptied depth would be other possibilities. I suspect that __R__. __sileacus__ would be reduced in arable soils in which pesticides would move rapidly and penetrate the deeper soil layers. Our study site was a pasture on clay-laom soil so that vertical distribution of pesticides would be more limited.

EFFECTS ON LINDANE, CARBARYL, AND CHLORPYRIFOS ON NON-TARGET SOIL ARTHROPOD COMMUNITIES

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INTRODUCTION

In an effort to reduce losses of high-value pine trees in campgrounds, parks and dooryards, lindane is used as a protectant spray in localized but heavy applications. The toxicity of lindane (and certain other insecticides) to bark beetles has been established (Lyon, 1971; Smith, Trostle and McCambridge, 1977). However, lindane's operational efficacy has been challenged (Dahlsten, 1976), and suspected environmental side effects have resulted in a rebuttable presumption against reregistration by the U. S. Environmental Protection Agency. Should reregistration be denied or failures prove widespread, possible alternatives to lindane include carbaryl and chlorpyrifos (Lyon, 1971; Smith et al., 1977).

Concern that splash and drift of bark beetle sprays disrupt the soil arthropod community directly under sprayed trees resulted in a cooperative research agreement between the U.S. Forest Service and the University of California. The ultimate concern is that a change in the arthropod community will affect litter decomposition and nutrient recycling. Although the importance of microarthropods in litter decomposition is not well understood, Harding and Stuttard (1974) concluded that it is greatest in pioneer and mor soils. The microarthropods disintegrate litter, which increases the surface area for fungal attack, and they mix the organic and mineral components of the soil (Edwards, Reichle and Crossley, 1977).

The study of lindane began in 1978 in a mature pine plantation (*Pinus ponderosa* Lawson), and a comparison of the effects of lindane, carbaryl and chlorpyrifos was initiated in 1979 in a stand of mature ponderosa pine forest.

METHODS

The initial study of lindane was started in 1978 at the U. S. Forest Service Institute of Forest Genetics, Placerville, California at 800 m elevation. Plots 3 m in diameter were sprayed with lindane at either of two rates, 1.13 g/m^2 or 11.3 g/m^2. The latter rate was 10 times the base rate which one might expect under a tree to which lindane carefully and legally was applied. The higher rate was to ensure an effect and to simulate an over-zealous application. Spray plot application rates were established on the assumption that 10 percent of the volume applied to a tree fell as splash or drift, and that 80 percent of that fell within 1.5 m of the center of the tree. Residue analyses of soil under treated trees confirmed the model.

One day prior to spray plot treatment and at 3, 9, 21, 45, 93, 141, and 381 days post-treatment soil cores were taken from the 11 replicates of each treatment. During 1978 2 cores 32 cm^2 x 7.6 cm deep were taken from each plot, however the last samples (at 381 days) were 20 cm^2 x 5.1 cm deep, 3 per plot. Extraction of the arthropods over a 4 day period followed Price's method (1973). All data analysis was of composite data from each plot.

In 1979 the following treatments were randomly assigned to 49 plots in the Challenge Experimental Forest, Challenge, California: chlorpyrifos at 5.22 g/m^2, 6 plots; chlorpyrifos at 26.1 g/m^2, 6 plots; lindane at 1.57 g/m^2, 6 plots; lindane at 7.83 g/m^2, 6 plots; carbaryl at 5.22 g/m^2, 6 plots; carbaryl at 26.1 g/m^2, 6 plots and 13 controls. These application rates were based on refined estimates of residues under trees treated in routine operations.

Statistical analyses were analysis of variance following Little and Hills (1978), the Games and Howell t-modification (Keselman and Rogan, 1978) and Kendall's tau following Ghent (1963).

I would like to acknowledge the taxonomic services of Drs. Roy A. Norton and Douglas W. Price and Ms. Barbara Wilson for identifications of the Cryptostigmata, Prostigmata and Mesostigmata, and Collembola, respectively. Drs. Michael I. Haverty and C. J. DeMars gave me helpful suggestions during the preparation of this paper. Funding for the research was provided by the U. S. Forest Service, Cooperative Research Agreement FS-PSW #50 and #68.

RESULTS

For the sake of clarity, only pretreatment and 45, 141 and 381 post-treatment data will be presented, and that as a percentage reduction below concurrent controls. Furthermore, only those taxa that were well represented will be discussed.

The general effects of lindane applied in the pine plantation can be seen in Table 1. The Collembola were reduced to a highly significant degree under the high application rate after 141 days and at both the high and low rate 381 days after application. Contrariwise, the Prostigmata were reduced to a highly significant degree after 45 days at both rates, showed strong signs of recovery after 141 days, and were very abundant 381 days post-treatment where the high rate was used. The Mesostigmata showed moderate (but not significant) reductions prior to 381 days, at which time there was an increase over control numbers in the low rate plots and a highly significant reduction in the high rate plots. The Cryptostigmata were reduced during all three periods, either significantly or highly significantly in all but one case. The category

TABLE 1. Percent reduction (increase) of arthropod groups following application of lindane at two spray treatment rates, 11 plots/treatment

	45 days		141 days		381 days	
	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2
Collembola	53	47	20	82[a/]	87	96
Prostigmata	40	62	12	23	23	(204)
Mesostigmata	38	53	25	57	(56)	85
Cryptostigmata	52	67	34	79	62	83
Others	16	25	58	89	44	70

[a/] Double underlining indicates statistical significance at the 1% level (single underlining, the 5% level) following transformation of counts to log (N+1).

which included all other arthropods showed the greatest effects after 141 days, but with a striking effect at the high rate even at 381 days.

The Collembola, most abundantly represented by the Entomobryidae and the Onychiuridae, showed a wide range of responses to lindane. The dramatic and lasting reduction of the Entomobryidae and the erratic reductions of the Onychiuridae, as well as the effects on other families as illustrated by Table 2.

The effects of lindane on the Prostigmata are given in Table 3 by families. The first five families show the most dramatic effects. All but the Tydeidae were severely reduced. The very abundant Tydeidae were eventually overabundant by 241 percent.

The Cryptostigmata offer the greatest opportunity to see the effects of lindane on the community as a whole. With 10 species (see Table 4) abundant enough for analysis of variance, a wide variety of responses were found. *Aphelacarus acarinus* (Berlese) and *Eobrachychthonius* sp. were severely affected. A progressive reduction was evidenced by *Sphaerochthonius* sp. and *Eramaeus* sp. However, *Scheloribates* sp. seemed to rebound from a slight initial reduction to overabundance. Overall, after 381 days, all but *Scheloribates* sp. were greatly reduced at the high rate and most were greatly reduced at the low rate.

Three quantitative measures of community structure were applied to the cryptostigmatid data; 1) mean number of species per plot, 2) the complemented Simpson's index, 3) Kendall's tau. The latter statistic is a rank correlation method advocated by Ghent (1963), but seldom used. It has the advantage that paired data are used, thereby preserving information content lost by the more widely used Simpson's index or the information theory indices.

TABLE 2. Percent reduction (increase) of Collembola following application of lindane at two spray treatment rates, 11 plots/treatment

	45 days		141 days		381 days	
	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2
Entomobryidae	74[a]	99	86	100	91	99
Isotomidae	70	41	50	96	35	88
Onychiuridae	15	39	(57)	43	83	97
Poduridae	28	16	33	74	77	63

[a] Double underlining indicates statistical significance at the 1% level (single underlining, the 5% level) following transformation of counts to log (N+1).

TABLE 3. Percent reduction (increase) of Prostigmata following application of lindane at two spray treatment rates, 11 plots/treatment

	45 days		141 days		381 days	
	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2
Nanorchestidae	82	100	87	100	86	97
Eupodidae	92	86	89	96	96	100
Tydeidae	30	54	(2)	2	24	(241)
Bdellidae	81	97	-	-	66	96
Cunaxidae	91	100	85	100	95	100
Cryptgnathidae	45	4	(3)	41	81	21
Raphignathidae	37	94	46	76	38	77
Caligonellidae	16	62	34	70	36	53
Stigmaeidae	38	(22)	(25)	(260)	30	25

[a] Double underlining indicates statistical significance at the 1% level (single underlining, the 5% level) following transformation of counts to log (N+1).

TABLE 4. Percent reduction (increase) of Cryptostigmata following application of lindane at two spray treatment rates, 11 plots/treatment

	45 days		141 days		381 days	
	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2	1.13 g/m^2	11.3 g/m^2
Aphelacarus acarinus	$\underline{79}$[a]	$\underline{\underline{99}}$	$\underline{\underline{97}}$	$\underline{\underline{99}}$	$\underline{\underline{97}}$	$\underline{\underline{99}}$
Sphaerochthonius sp.	6	12	25	71	73	$\underline{85}$
Eobrachythonius sp.	$\underline{\underline{96}}$	$\underline{\underline{97}}$	-	-	95	100
Epidamaeus sp.	(117)	60	38	$\underline{\underline{93}}$	65	$\underline{\underline{98}}$
Eramaeus sp.	64	$\underline{\underline{84}}$	$\underline{75}$	$\underline{\underline{99}}$	$\underline{\underline{89}}$	$\underline{\underline{100}}$
E. stiktos	58	$\underline{\underline{91}}$	-	-	51	$\underline{94}$
Autogneta sp.	56	38	54	$\underline{87}$	52	$\underline{98}$
Opiella nova	(200)	66	9	53	9	78
Scheloribates sp.	36	49	(108)	45	(172)	(160)
Zachvatkinibates sp.	92	$\underline{98}$	81	$\underline{\underline{100}}$	-	-

[a] Double underlining indicates statistical significance at the 1% level (single underlining, the 5% level) following transformation of counts to log (N+1).

Pretreatment samples provide data on species richness and heterogeneity as well as do concurrent controls (Table 5). A slight decline occurred in mean number of species per plot in the low rate plots, and a sharp decline in the high rate plots. Species diversity as measured by Simpson's index was very uniform prior to spray treatment, and was slightly depressed in the control plots at 141 days (late summer). At the low rate Simpson's index changed very little until the 381 day sampling. However, at the high rate there was a steady decline throughout the post-treatment sampling.

Rank correlation of the abundances of the cryptostigmatid species between controls and the two spray treatments are given in the last two columns of Table 5. Note the difference in the two statistics prior to spraying. There was a relatively slight decline in the correlation in the comparison with low rate plots and a dramatic decline in the high rate plots.

TABLE 5. Cryptostigmatid species richness, heterogeneity and species rank correlation arranged according to four sampling periods and three treatments

	Richness (Mean species per plot)			Heterogeneity (Complemented Simpson's)			Rank Correlation (Kendall's tau)	
	Control	1.13 g/m^2	11.3 g/m^2	Control	1.13 g/m^2	11.3 g/m^2	Control vs. 1.13 g/m^2	Control vs. 11.3 g/m^2
1 day pre-treatment	10.5	10.7	9.5	.86	.88	.87[b]	.66	.74[b]
45 days post-treatment	12.8	11.6	8.2[a]	.87	.82	.69	.57	.33
141 days post-treatment	11.6	9.6	4.4	.75	.73	.51	.61	.47
381 days post-treatment	11.6	8.5	4.1	.89	.28	.28	.46	.26

[a] Double underlining indicates statistical significance at the 1% level (single underlining, the 5% level) following transformation of counts to log (N+1).

[b] Fiducial limits not set.

Comparison of the effects of lindane, carbaryl and chlorpyrifos on soil arthropods under pine is in progress in a mature forest setting. The fauna is more diverse than in the plantation study described above, but the abundances of given species are lower. Table 6 reflects this situation, for in it are listed only the 6 cryptostigmatid species that were abundant enough for analysis of variance. After 40 days it appears that chlorpyrifos had a relatively slight effect, that lindane had a strong negative effect and carbaryl had a mixed, but often positive effect. At the same time chlorpyrifos had strong and statistically significant effect on the miscellaneous arthropods and the prostigmata as a group, while neither lindane nor carbaryl had a significant effect. Much of the effect on the Prostigmata was the result of the sensitivity of the Tydeidae. The Mesostigmata were surprisingly rare during this time.

DISCUSSION

Years may pass before soil fertility problems resulting from persistent pesticides use in forests become evident as was pointed out by Thompson and Edwards (1974). That is the underlying thought for this discussion.

Interpretation of a body of data arranged by taxonomic categories should not be done line by line. Nor should the traditional 5% level of significance be rigidly imposed on data from species that are notorious for contagious distributions, data transformation notwithstanding.

Comparison between the lindane experiment and the Chlorpyrifos-lindane-carbaryl experiment is probably justified despite 7.6 cm core depths in one, and 5.1 cm depths in the other. However, the single point in time and reduced replication in the second experiment prevent that data from standing alone.

Lindane effects

A long-term effect by lindane on all major groups is evident. Therefore, annual applications of lindane for bark beetles would certainly cause a continuous depression in the numbers of most species, and they would probably have a cumulative effect.

The contrasting effects of the two application rates on the Prostigmata, for which the Tydeidae hold the statistical explanation, most likely has a biological explanation in the Mesostigmata data. The average density of mesostigs increased in the low rate plots after a year had gone by, but density was still declining in the high rate plots. Although all of the mesostig data were sparse, there was a strong suggestion of a phytoseiid explosion relative to earlier levels. A differential effect of lindane on predaceous mesostigs seems to explain the tydeid numbers.

The ongoing and increasing effect on the Collembola seems quite straightforward. Family differences through time could be explained by

TABLE 6. Percent reduction (increase) of Cryptostigmata 40 days following application of three materials at two rates each, 13 control plots, 6 each of spray treatment

	chlorpyrifos		lindane		carbaryl	
	5.22 g/m^2	26.1 g/m^2	1.57 g/m^2	7.83 g/m^2	5.22 g/m^2	26.1 g/m^2
Joshuella sp.	19	43	80	79	64	(176)
Eramaeus sp.	38	65	90	100	61	41
Carabodes sp.	(149)	52	100	44	94	71
Scheloribates sp. 1	42	34	65	57	6	(239)
Scheloribates sp. 2	57	81	89	98	(121)	63
Neoribates sp.	14	40	84	96	(314)	(218)
Total Cryptostigmata	30	63	82	85	16	(153)

1) downward movement of residues, 2) seasonal movement of the collembolans, 3) community dynamics. I would expect that a combination of the last two is most likely.

Quantitative analysis of community structure, as affected by lindane, was limited to the cryptostig component of the soil community. For the cryptostigs there was greater depth of data and identification to species. "Direct species counts, while lacking theoretical elegance, provide one of the simplest, most practical, and most objective measures of species richness" (Peet, 1974). Using that measure I found very slight differences in counts among the plots before treatment and declines in richness at both spray treat rates throughout the study, whereas the index remained high in the concurrent control plots.

Simpson's index, as opposed to the Shannon index and others based on information theory, is most sensitive to changes in the abundant species (Peet, 1974). I have made the conservative assumption that the more abundant cryptostigs are more important to community structure and fertility than the uncommon species. With one exception, Simpson's index ranged from 0.86 to 0.89 in the pre-treatment and concurrent control plots. At 381 days both spray rates had an index of 0.28 pointing to a long-term decline of population heterogeneity following lindane application.

Rank correlation of the abundances of species preserves information content by keeping species names associated with items in the frequency distributions from each treatment. This is done by neither the Shannon index nor Simpson's index. The overall trend of correlations was a decline over time. The significance of the slight upturn for both application rates at the 141 day point is uncertain. It may reflect a greater sensitivity or some aspect of community structure not measured by Simpson's index. However, by this measure there is also a change in community structure.

Chlorpyrifos and carbaryl effects

The effect of chlorpyrifos and carbaryl on the cryptostigs 40 days after application are quite different from each other, and from lindane (Table 6). Chlorpyrifos seems to have a limited negative effect, and carbaryl a very mixed effect. The greater number of positive effects and only moderate negative effects caused by the high application rate of carbaryl than caused by the lower rate, suggest that there may be a general increase of prey because of predator mortality. Yet the slow reproductive cycle of the cryptostigs would require fortuitious timing of the applications for this to show up in just 40 days. Until the fall season's collections are in this question will be left unresolved.

CONCLUSIONS

Lindane residues had a pronounced, lasting and increasing effect on the soil fauna through 381 days. The effects include changes in total numbers and in the community structure. The two alternate materials, chlorpyrifos and carbaryl, have very different effects on the dominant group, the cryptostigmata, at 40 days post-treatment.

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QUESTIONS and COMMENTS

G. BENGTSSON: Using diversity indicies, e.g. Simpson's for describing changes in species composition (number, diversity) might be obscured by changes in evenness which the indicies have not been developed to describe. Fitting data to models for species abundance distribution is another deductive method. Why do you prefer to use indicies in this work?

J.B. HOY: I chose Simpson's index because it emphasizes the more abundant species and Kendall's rank correlation method because it retains information content lost by the other methods. Should there be inversions in the ranks Kendall's tau will detect changes missed by the index. I cannot discuss the fine points of the Shannon index, but have relied on Peet's (1974) review.

F. GOULD: Were any of the increases in abundances significant statistically?

J.B. HOY: Only the tydeids. They increased by 241%, a figure that was significant at the 5% level.

EFFECTS OF CARBOFURAN ON THE SOIL MICROARTHROPOD COMMUNITY IN A CORNFIELD

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INTRODUCTION

Carbofuran, a carbamate insecticide, was introduced in 1967 by the Niagara Chemical Division, F.M.C., under the trade name Furadan$^{(R)}$. Granular carbofuran, applied in-row at corn planting, is used extensively in Ontario for control of the northern corn rootworm, Diabrotica longicornis (Say).

Although the acute toxic effects of carbofuran to earthworms have been well documented (Stenersen, Gilman and Vardanis 1973; Tomlin and Gore 1974), its effect on the beneficial soil microarthropod community is not well understood. The important role of these microarthropods in the decomposition process of organic matter has been reviewed by Edwards, Reichle and Crossley (1970) and Edwards (1974). Any agricultural practice, including the use of insecticides, which interferes with the composition of the decomposer community or shifts its component populations' equilibria may result in reduced litter decomposition which could affect soil fertility.

Thompson and Edwards (1974) have reviewed the effects of pesticides on non-target soil fauna. Martin (1978) has reported the effect of carbofuran (2.24 kg a.i./ha) on soil arthropods when applied as granules to the surface of a New Zealand pasture.

As part of a study to determine the effect of carbofuran on the decomposer community, soil cores were taken in a cornfield and the resident microarthropods analyzed in the laboratory for population differences due to carbofuran treatment.

MATERIALS AND METHODS

The experimental site was a plot (120 x 40 m) of sandy loam soil in a 12 ha field of continuous corn under regular tillage and management at the Arkell Research Station, near Guelph, Ontario. Soil cores (5 cm diam. x 15 cm deep) were taken randomly from within the rows of a carbofuran 10 G row-treated (1.12 kg a.i./ha, the recommended rate in Ontario) and a control plot in the cornfield. In 1977, 10 soil cores per treatment were taken at 4, 16 and 24 weeks after planting/treatment day (May 10); in 1978, 12 cores per treatment were taken at 2 weeks pre-treatment, at treatment day (May 23), and at 2, 6, 10, 14, 18 and 22 weeks post-treatment.

Microarthropods in the soil cores were extracted in the laboratory by modified Tullgren funnels as described by Tomlin (1977). Extraction was completed in 72 hours with the animals being collected in glycerol: ethanol:water (5:70:25). The arthropods were subsequently counted and identified to family level for Collembola and suborder for Acari, using a dissecting microscope. The numbers of specimens for each of these major taxa from treated and control plot cores were subjected to analysis of variance for each sampling date. Logarithmic transformation of the data was used to stabilize the high variance due to contagious distributions of most of these arthropods.

RESULTS AND DISCUSSION

The proportions of the component populations of the soil arthropod fauna in the cornfield during the growing season are shown for 1977 (FIGURE 1) and 1978 (FIGURE 2). More than 90% of the arthropods recovered from each sampling date were mites and springtails. The predominant genera of Acari and Collembola identified from the cornfield are listed in TABLE 1.

TABLES 2-7 (Appendix A) summarize the effects of carbofuran on various components of the soil arthropod fauna on successive sampling dates in 1977 and 1978.

Differences between the control and treated cores were not consistent over the sampling period or between years. The total number of arthropods per core differed significantly ($P<0.01$) on only one sampling date in 1977 (9 June, 4 weeks post-treatment) and one date in 1978 (25 October, 22 weeks post-treatment). On both these dates the number of arthropods in the treated plot was approximately twice the size of that in the control.

The myriapods, predominantly pauropods, symphylids, and diplopods comprised consistently less than 10% of the total arthropod population, typically 2 to 5 per core except on September 1, 1978 when 12 per core were recorded for the control plot. On that date the mean number of pauropods per core in the control was 4.5 times greater than in the treated plot.

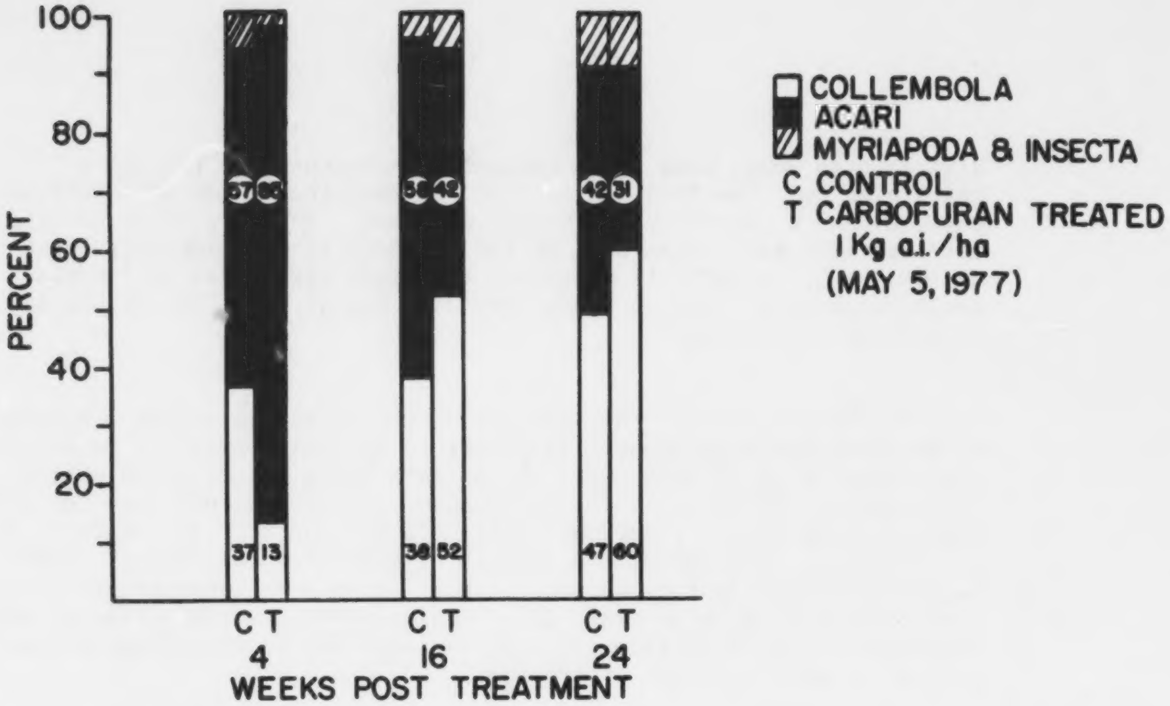

FIGURE 1. Proportions of the component populations of soil microarthropods in control and carbofuran treated plots of Arkell cornfield 1977.

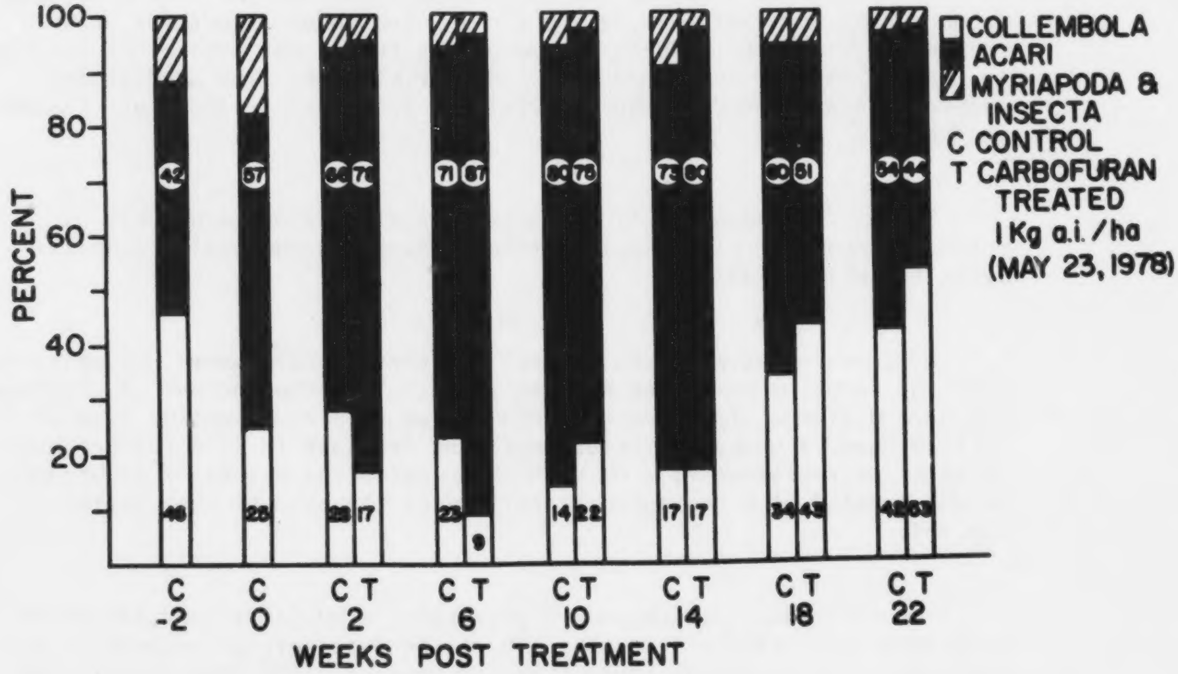

FIGURE 2. Proportions of the component populations of soil microarthropods in control and carbofuran treated plots of Arkell cornfield 1978.

TABLE 1. The major families and genera of Acari and Collembola recovered from the Arkell cornfield soil.

ACARI	FAMILY	GENUS
PROSTIGMATA		
	Pygmephoridae	Bakerdania
	Tarsonemidae	Tarsonemus
	Scutacaridae	Scutacarus
	Nanorchestidae	Speleorchestes
	Tydeidae	Tydeus
	Eupodidae	Eupodes
MESOSTIGMATA		
	Ascidae	Arctoseius
	Ascidae	Protogamasellus
	Rhodacaridae	Rhodacarellus
	Digamasellidae	Dendrolaelaps
	Laelapidae	Hypoaspis
	Parasitidae	Pergamasus
CRYPTOSTIGMATA		
	Oribatulidae	Scheloribates
	Oribatulidae	Zygoribatula
	Oppiidae	Oppia
	Oppiidae	Oppiella
	Tectocephidae	Tectocepheus
ASTIGMATA		
	Acaridae	Acarus
	Acaridae	Rhizoglyphus
COLLEMBOLA		
	Isotomidae	Isotoma notabilis Schaffer
	Isotomidae	Proisotoma minuta (Tullberg)
	Isotomidae	Folsomides parvus Folsom
	Entomobryidae	Lepidocyrtus cyaneus Tullberg
	Entomobryidae	Pseudosinella sp.
	Onychiuridae	Onychiurus armatus (Tullberg)

The pterygote insects, mainly larvae of Diptera and Coleoptera, were consistently less than 4% of the total arthropod population (1 to 2 per core). No differences due to treatment were observed, particularly as no corn rootworm population was found in the cornfield.

The major differences observed between the control and treated plots involved the Acari and Collembola; the most obvious difference was the larger prostigmatid mite population in the treated plot. This increase was made up largely from the mite Bakerdania sp. (Pygmephoridae) which occurred in consistently higher numbers after carbofuran treatment (at 4 weeks in 1977 and 2 and 6 weeks post-treatment in 1978). By 16 and 18 weeks post-treatment, in 1977 and 1978 respectively, this mite had shown a significant ($P<0.05$) decline in population in the treated compared to the control plot.

The mesostigmatid mites (predominantly predacious) showed a significant decline ($P<0.05$) in both years following carbofuran treatment, while the largely saprophagous cryptostigmatid mites showed a significant seasonal increase after treatment in both years. The astigmatid mites were present in very low numbers (1 to 3 per core).

Among the collembolan families, the Isotomidae and Entomobryidae frequently showed an inverse relationship with each other, such that after carbofuran treatment the isotomid population decreased while the entomobryid population increased. The onychiurid population initially was small, but by 18 weeks post-treatment in 1978, it had increased and was significantly ($P<0.01$) greater in the treated than in the control plot. An interesting observation at 22 weeks post-treatment (1978) was the significant ($P<0.01$) increase in the populations of the Isotomidae and Entomobryidae in the treated plot. The families, Poduridae and Sminthuridae were recorded at very low densities of less than one per core.

Most of the population changes observed following carbofuran treatment agree with those of Martin (1978). He noted significant increases, at 7 weeks after carbofuran treatment, in certain Prostigmata (Pygmephoridae, Scutacaridae, Tarsonemidae: *Xenotarsoneumus*, all $P<0.01$) and Cryptostigmata (Oribatulidae: *Multoribates*, $P<0.05$). A significant decrease in population of 2 species of Mesostigmata (Ascidae: *Arctoseius*, Veigaiidae: *Veigaia*, both $P<0.01$) was also found at 7 weeks post-treatment. Among the Collembola present, Martin records a significant increase ($P<0.05$) in one isotomid (*Isotomurus* sp.) at 20 weeks post-treatment. Our initial decline in the isotomid population agrees with Tomlin (1975) who found carbofuran to be very toxic to *Folsomia candida* (Isotomidae) in a laboratory study.

A predator-prey relationship is suggested by our results, since it is hypothesized that the saprophagous Prostigmata and Cryptostigmata increase as a result of the decline in predacious Mesostigmata. Predatory mites with greater mobility and metabolic rate are more susceptible to insecticides than saprophagous mites (Edwards 1965). Also, since carbofuran has been shown to be very toxic to earthworms (Stenersen et al. 1973), the hypothesis of Martin (1978) warrants further investigation, that the presence of a large biomass of dead earthworms plus all the food in the soil not consumed by these worms could account for high populations of detritivorous mite and springtail species after treatment.

Martin noted that nearly all the species most affected by carbofuran inhabit the litter and surface layers of the soil. Future studies should include division of the soil core into horizons before extraction and analysis, as well as study of carbofuran penetration into the soil.

CONCLUSIONS

The overall results of this soil microarthropod survey are difficult to interpret. Although fluctuations in various component populations were observed due to treatment there is no substantial reduction in the total fauna or its composition by autumn. More drastic population fluctuations can be expected from the effects of cultivation and the addition of organic manure (Edwards and Lofty 1969). It is therefore concluded that at current approved application rates, carbofuran had no observable long term detrimental effects on the microarthropod decomposer community. Hence, it is considered unlikely that a significant effect on litter decomposition in the cornfield soil occurred.

ACKNOWLEDGMENTS

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Contribution No. 765, Research Institute, Agriculture Canada, London.

APPENDIX A

TABLE 2. Mean number of major arthropod taxa per soil core (n=10) in a carbofuran treated (T)(May 5) and control (C) plot of Arkell cornfield 1977

	Weeks Post-treatment					
	4		16		24	
	(9.6.77)		(2.9.77)		(28.10.77)	
	C	T	C	T	C	T
TOTAL ARTHROPODS	69.1	131.4**	84.5	53.5	52.5	67.1
ACARI	39.6	111.4*	48.7	22.4*	21.8	21.1
COLLEMBOLA	25.6	16.4	31.9	27.9	25.9	39.9
MYRIAPODA	2.1	2.1	2.4	2.0	3.2	4.7
INSECTA	1.8	1.5	1.5	1.2	1.6	1.4

Significant difference * $P < 0.05$; ** $P < 0.01$

TABLE 3. Mean number of Acari per soil core (n=10) in a carbofuran treated (T)(May 5) and control (C) plot of Arkell cornfield 1977

	Weeks Post-treatment					
	4		16		24	
	(9.6.77)		(2.9.77)		(28.10.77)	
	C	T	C	T	C	T
ACARI	39.6	111.4*	48.7	22.4*	21.8	21.1
PROSTIGMATA	27.2	104.8**	33.6	14.5*	12.9	10.7
MESOSTIGMATA	11.7	4.5*	10.1	3.4**	4.9	4.9
ASTIGMATA	0.7	0.8	2.9	1.5	3.0	2.7
CRYPTOSTIGMATA	0	1.3**	2.1	3.0	1.0	2.8

Significant difference - * $P < 0.05$; ** $P < 0.01$

TABLE 4. Mean number of Collembola per soil core (n=10) in a carbofuran treated (T)(May 5) and control (C) plot of Arkell cornfield 1977

	Weeks Post-treatment					
	4		16		24	
	(9.6.77)		(2.9.77)		(28.10.77)	
	C	T	C	T	C	T
COLLEMBOLA	25.6	16.4	31.9	27.9	25.9	39.9
ISOTOMIDAE	10.0	1.7**	13.2	7.1	12.9	24.2
ENTOMOBRYIDAE	8.5	9.2	11.6	15.4	10.5	11.3
ONYCHIURIDAE	6.0	5.4	6.1	4.8	1.9	3.9
SMINTHURIDAE	0.8	0	0.7	0.6	0.5	0.5
PODURIDAE	0.3	0.1	0.3	0	0.1	0

Significant difference - ** P<0.01

TABLE 5. Mean number of major arthropod taxa per soil core (n-12) in carbofuran treated (T)(May 23) and control (C) plot of Arkell cornfield 1978.

	Weeks Post-treatment											
	2 (9.6.78)		6 (6.7.78)		10 (3.8.78)		14 (1.9.78)		18 (28.9.78)		22 (25.10.78)	
	C	T	C	T	C	T	C	T	C	T	C	T
TOTAL ARTHROPODS	100.0	105.2	133.7	127.3	145.1	153.7	186.2	198.8	118.1	99.9	73.4	146.7**
ACARI	65.5	82.4	95.4	110.7	116.2	116.7	136.2	158.5	70.7	50.9	39.4	64.2*
COLLEMBOLA	28.0	17.6	30.8	10.8*	19.7	33.4	32.0	33.6	40.0	42.8	30.7	77.4**
MYRIAPODA	2.5	1.8	2.4	1.3	5.2	2.7	12.4	3.7	4.8	4.6	1.9	4.2
INSECTA	3.9	3.4	5.1	4.5	4.0	2.9	5.6	3.0	2.6	1.6	1.4	0.9

Significant difference - * P<0.05; ** P<0.01

TABLE 6. Mean number of Acari per soil core (n=12) in carbofuran treated (T)(May 23) and control (C) plot of Arkell cornfield 1978.

	Weeks Post-treatment											
	2 (9.6.78)		6 (6.7.78)		10 (3.8.78)		14 (1.9.78)		18 (28.9.78)		22 (25.10.78)	
	C	T	C	T	C	T	C	T	C	T	C	T
ACARI	65.6	82.4	95.4	110.7	116.2	116.7	136.2	158.5	70.7	50.9	39.4	64.2*
PROSTIGMATA	49.8	73.2	49.6	74.7	76.7	78.7	113.4	127.9	57.4	32.6*	28.2	41.3
MESOSTIGMATA	13.0	6.2*	33.6	26.5	37.9	30.0	17.8	16.9	10.0	3.5*	6.5	5.0
ASTIGMATA	2.4	2.1	0.3	2.7	0.8	1.3	2.4	1.4	1.2	0.5	1.4	2.8
CRYPTOSTIGMATA	0.4	0.9	1.9	6.8*	0.8	6.7**	2.6	12.3	2.1	14.3*	3.3	15.1**

Significant difference - * P<0.05; ** P<0.01

TABLE 7. Mean number of Collembola per soil core (n=12) in carbofuran treated (T)(May 23) and control (C) plot of Arkell cornfield 1978

	Weeks Post-treatment											
	2 (9.6.78)		6 (6.7.78)		10 (3.8.78)		14 (1.9.78)		18 (28.9.78)		22 (25.10.78)	
	C	T	C	T	C	T	C	T	C	T	C	T
COLLEMBOLA	28.0	17.6	30.8	10.8*	19.7	33.4	32.0	33.6	40.0	42.8	30.7	77.4**
ISOTOMIDAE	21.2	7.8	18.2	5.1*	10.4	6.9	9.8	8.2	13.1	6.4	7.9	24.8**
ENTOMOBRYIDAE	3.8	6.9	3.4	3.7	4.6	21.2*	10.4	15.4	17.7	15.9	9.2	30.2**
ONYCHIURIDAE	2.0	2.1	7.2	2.0	4.5	5.3	11.2	10.0	8.8	20.2**	12.9	21.3
SMINTHURIDAE	0.5	0.7	0.1	0	0	0	0	0	0.2	0.3	0.6	1.0
PODURIDAE	0.5	0.1	1.9	0	0.2	0	0.6	0	0.2	0	0.1	0.1

Significant difference - * P<0.05; ** P<0.01

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QUESTIONS and COMMENTS

M.S. GHILAROV: How do you explain the increase of some groups of microarthropods after the insecticide treatment? In our experiments with DDT dusting of natural coniferous forests in Siberia, the observed effect of a temporary decrease of collembolan population density followed by a great increase in population was related to the suppression by treatment of predators (Mesostigmata and Coleoptera).

A.B. BROADBENT: I can only hypothesize at this time. Two reasonable explanations are: firstly, the suppression of predators (particularly Mesostigmata) gave rise to an increase in their prey (particularly Prostigmata and

Collembola) and secondly, due to the very toxic effect of carbofuran to earthworms, and therefore the presence of a large biomass of dead worms, plus all the food in the soil not consumed by these worms, a larger population of saprophagous animals was supported. The latter hypothesis was proposed by Martin (1978).

S.B. HILL: The speaker has concluded that because no reduction in total fauna or its composition was observed by autumn, therefore there were no long-term detrimental effects on the microarthropod decomposer community due to carbofuran treatment. When in fact, an increase in population of certain groups was observed 22 weeks post-treatment in 1978, can it still be concluded that no detrimental effects on the community or its litter decomposition processes occurred? As ecologists, we mustn't assume that "more is better." Would the speaker please comment.

A.B. BROADBENT: Since no reduction in the populations of saprophagous animals, in particular, was observed by late season, I have concluded that no long-term detrimental effects on the community or litter decomposition processes occurred after carbofuran treatment. This rather tentative conclusion is supported by data from a litterbag study conducted concurrently in the same plots. The rates of cornleaf decomposition were monitored and we found that although a lag in response was observed initially, by autumn no difference in rate was noted between carbofuran treated and control plots.

C.A. EDWARDS: Following mention by the speaker of the effect of carbofuran on organic matter breakdown, I should like to comment that Dr. J.F. McBrayer and I investigated the effects of phorate on corn litter breakdown in an Indiana field and found a significant depression in decomposition rate after treatment.

INFLUENCE OF APPLICATION OF A FUNGICIDE, AN INSECTICIDE, AND COMPOST UPON SOIL BIOTIC COMMUNITY

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INTRODUCTION

Soil fauna and soil flora constitute soil biotic community or edaphon. Herbivorous and fungivorous animals consume leaf and woody litter, fungi and humus and eject large amount of fecal pellets giving rise to the crumby structure of the soil. These bring about the breakdown of dead plant bodies, mixing of them with soil, increase and maintenance of porosity, aeration and water capacity of the soil, which are closely related to the increase and maintenance of the microbial activity. Predation by microbivorous animals is related to the control of microbial numbers and increase in net microbial production. Movement of soil fauna facilitates the dissemination of bodies and spores of microbes. Thus the soil fauna plays a catalytic role against microbial activity and is related to the increase and maintenance of soil fertility.

The purpose of the present study is to pursue the changes in soil fauna and soil microbes in the experimental field where insecticide, fungicide and compost are supplied singly and in combination. This study was made in joint research with Prof. Takai and his group of the University of Tokyo, who engaged in the subjects other than soil fauna.

METHODS

Six kinds of experimental plots were set up in the experimental field of the Faculty of Agriculture of the University of Tokyo as shown in TABLE 1. Grasses and herbs in the plots were removed. Compost, a

TABLE 1. Experimental plots.

Year	April 1973 to March 1974	May 1974 to December 1977	
Plots	Control	A	Control
		B	Compost 3 $\text{kg}\cdot\text{m}^{-2}$
		C	TPN 40 ppm
	BHC 10 ppm	D	γBHC 10 ppm
	Aldrin 10 ppm	E	TPN 40 ppm + γBHC 10 ppm
		F	Compost + TPN + γBHC (Same Conc.)

fungicide TPN (Daconil) and an insecticide γBHC were supplied singly or mixed to the plots in the amounts shown in TABLE 1. The size of a soil sample core for small Arthropoda was 20 cm^2 in surface area, 5 cm deep and 100 cm^3 in volume. Ten of them were taken from each plot in 1974, and in 1975 and afterwards five soil cores were taken from carefully stirred 3500 cm^3 of soil taken from five places in each plot. Extraction of animals with Tullgren funnels was continued for 48 hours. A soil core for small hygrophilous animals such as Enchytraeidae, Nematoda and Rotifera was (2.5 cm x 2.5 cm x 4 cm) = 25 cm^3 in volume. Ten of them were taken from each plot in 1974 and 1975 and afterwards five were taken from above stirred soil. Extraction of animals with Baermann funnels was continued for 48 hours.

The survey of soil macrofauna was made only once in 1977 at the end of the period of experiment by hand sorting, because the area of the experimental plot was so small that each survey may injure the plot so much and cause the decrease in density and biomass which are detrimental for this study. Number of taxonomic groups (families and orders) and of individuals of macro-herbivores and macro-predators in 40500 cm^3 of soil in each plot were counted.

RESULTS

Main taxonomic groups extracted were Cryptostigmata, other Acari, Collembola, Diplura, Enchytraeidae, Nematoda and Rotifera (Bdelloidea). Besides these, Diptera larva, Protura, Symphyla and Tardigrada often appeared in small numbers. The numbers of these taxonomic groups were smaller than those in the soil of forests in Tokyo. It was noticeable that Pseudoscorpionida, Isopoda, Myriapoda, Copepoda and Turbellaria were lacking in the experimental plots. Changes in numbers of extracted animals are shown in APPENDIX A to F. Numbers of taxonomic groups and those of individuals of macro-herbivores and macro-predators are shown in TABLE 2. From the data shown in APPENDIX and TABLE 2, the following results could be introduced.

TABLE 2. Number of taxonomic groups and individuals of soil macrofauna. (Nov. 31 to Dec. 1, 1977)

		A	B	C	D	E	F
		Control	Compost	TPN	γBHC	T·B	C·T·B
Number of taxonomic groups	Macro-herbivores	4	10	1	4	1	5
	Macro-predators	5	10	3	4	0	3
	Total macrofauna	10	22	4	8	1	8
Number of individuals	Macro-herbivores	10	71	3	14	6	29
	Macro-predators	44	134	25	7	0	6
	Total macrofauna	55	207	28	21	6	35

Changes in numbers of small soil animals

Control plot (A)

Densities of soil animals of the control plot were lower than those of the forest soils in Tokyo in general. Number of Nematoda was about one tenth of that of the latter. But the patterns of seasonal changes in numbers are similar to those seen in natural soils of Tokyo districts. In the summer of 1975, the air temperature was unusually high and the precipitation was small. The soil of the plot was very dry and numbers of soil animals reduced.

Compost plot (B)

Numbers of all six main animal groups, namely Collembola, Cryptostigmata, other Acari, Enchytraeidae, Nematoda and Rotifera increased indicating marked influence of the supply of compost.

Fungicide plot (C)

After three years continuous supply of TPN, numbers of all of the six main groups were diminished. Especially remarkable was the diminution in hygrophilous animals as Enchytraeidae, Nematoda and Rotifera.

Insecticide plot (D)

Numbers of Arthropoda, namely, Cryptostigmata, other Acari and Collembola were reduced. But the insecticide effect of γBHC on Collembola seemed to disappear after six months from the time of supply. Numbers of Enchytraeidae, Nematoda and Rotifera did not decrease but increased though this tendency was not clear in Nematoda in 1976. According to the study of Yang and Takai, The amount of γBHC had reduced to 30 to 10 % after one year from the supply to the soil.

TPN + γBHC plot (E)

All of the animal groups were remarckably influenced by the combined use of these fungicide and insecticide. Especially small Arthropoda were almost destructed by continuous combined supply. According to the study of Yang and Takai, the rate of decomposition of TPN and γBHC was reduced in this plot. In this experimental plot, an insecticide Aldrin was supplied in May 1973. A part of it changed to Dieldrin, and 75 to 90 % of them remained till one year later. It seems that there was influence of these two compounds on decrease in animals.

Compost + TPN + γBHC plot (F)

In 1974, numbers of Collembola, Enchytraeidae, Nematoda and Rotifera became larger than those in plot E, and in 1975 the same trend was seen in Nematoda, Enchytraeidae and though less remarkable in Collembola, suggesting the existence of function of compost to reduce the detrimental effect of TPN and γ BHC. But in 1976 this trend was seen only in Nematoda. It seems that in this plot the detrimental effect of three years combined use of TPN, γ BHC and of Aldrin used in 1973 exceeded the easing effect of supply of compost.

Changes in numbers of soil macrofauna

At the end of four years experiment, numbers of taxonomic groups of soil macrofauna was the largest in the compost plot, followed by the control plot and the least in the combination plot of TPN and γ BHC as seen in TABLE 2. It is also noteworthy that the number in F plot exceeded that of the plot E and C, suggesting the easing effect of supply of compost. Numbers of individuals of macrofauna was also the largest in the compost plot, followed by the control plot, the least in the plot of combimation of TPN and γ BHC. And the number in F plot exceeded that of E, C, and D. Thus the patterns of changes in numbers of Taxonomic groups representing the degree of community diversity and of individuals were almost the same.

DISCUSSION

The results of the experiments indicated that there were detrimental effects of continuing and combined use of TPN and γBHC against all of the soil fauna, and that the supply of TPN generally reduced numbers of small and large soil animals, while the supply of γBHC did not reduce the numbers of Enchytraeidae, Nematoda, Rotifera, but increased them. The supply of compost increased all the groups of the soil fauna concerned, and eased the detrimental effect of the supply of combined TPN and γBHC to some extent. These general trends were already recognized in 1974, the first year of the period of this study, and some discussions were made (Kitazawa and Kitazawa 1975).

The relation between changes in numbers of soil fauna and those of microbes

The changes in numbers of microbes, soil respiration and dehydrogenase activity in the soil of the same experimental plots were studied (Takai and Yang 1975), (Takai 1977). The relations between changes in numbers of soil fauna and those of soil microbes were taken into consideration. The results **in soil microbes are summarized as follows:**

Compost plot (B)

The supply of compost increased numbers of fungi, total bacteria and gram-negative bacteria to some extent, and also increased rates of soil respiration and dehydrogenase activity of the soil.

TPN plot (C)

The supply of TPN decreased numbers of fungi and spore-forming bacteria, but increased numbers of total bacteria, especially remarkably increased those of TPN-resistant gram-negative bacteria. It decreased rates of soil respiration and dehydrogenase activity of the soil.

γ BHC plot (D)

No marked influence of supply of γ BHC upon numbers of microbes, soil respiration and dehydrogenase activity was recognized. However, the continuous use of it increased numbers of gram-negative bacteria a little.

TPN + γ BHC plot (E)

The joint supply of TPN and γ BHC decreased numbers of fungi. But it increased the number of total bacteria a little and increased markedly that of gram-negative bacteria.

Compost + TPN + γBHC plot (F)

The joint supply of compost, TPN and γBHC eased the decreasing activity of TPN to the number of soil fungi and soil respiration rate, and accerelated the increasing effect of TPN and γBHC on the nembers of total bacteria and gram-negative bacteria.

The relations among effects of compost, TPN, γBHC on numbers of soil fauna, soil microbes and rates of soil respiration and dehydrogenase activity in the soil, were diagrammatically summarized in FIGURE 1.

More precise reports on microbes, microbial activity, decomposition and residue of chemical compounds will be published soon by Takai, Wada, Yang and Mukai.

SUMMARY

The effects of compost, a fungicide TPN, and an insecticide γBHC, supplied singly or combined, on numbers of soil animals were studied for four years, and the changes in them were discussed in relation to the changes in numbers of soil microbes, rate of soil respiration and dehydrogenase activity in the soil which were studied in the same experimental plots by Takai and others. The outline of the results were diagrammatically summarized in FIGURE 1.

APPENDIX A. Numbers of small soil animals extracted with Tullgren funnels. No./100 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 15 and 16 May, 1974.

1974	11 MAY	20 MAY	1 JUNE	15 JUNE	15 JULY	19 SEPT.	6 DEC.
	Collembola						
A	8.8±2.0	27.0±3.9	21.7±3.6	7.3±1.2	8.3±1.6	10.8±3.8	9.9±3.7
B	8.8±2.0	19.3±2.4	25.8±2.2	20.4±3.3	11.2±2.1	16.3±2.3	18.0±3.4
C	11.1±2.23	6.7±2.4	3.6±2.3	2.9±0.8	1.7±0.8	1.2±0.3	10.4±2.6
D	3.5±1.35	4.0±0.7	1.3±0.8	0.5±0.2	4.8±1.5	3.9±1.2	20.8±4.2
E	2.0±1.05	2.6±0.9	0	0	2.0±0.7	2.2±0.8	10.6±3.4
F	2.0±1.05	0	0.2±0.13	1.2±0.6	8.8±3.3	6.3±3.5	36.2±8.7
	Cryptostigmata						
A	6.3±1.1	1.5±0.5	2.5±0.7	1.7±0.8	1.5±0.5	10.6±4.9	1.5±0.4
B	6.3±1.1	1.7±0.4	2.4±1.0	3.9±0.9	3.9±0.2	15.1±2.4	2.0±0.7
C	9.0±1.5	1.3±0.5	1.5±0.4	1.2±0.9	0.7±0.3	1.2±0.8	0.5±0.3
D	0	0	0.1±0.1	0	0.1±0.1	0	0.5±0.3
E	0.1±0.1	0.1±0.1	0.5±0.5	0	0	0	0
F	0.1±0.1	0	0.1±0.1	0	0	0	0
	Other Acari						
A	10.8±3.0	3.8±0.5	3.8±0.7	2.9±0.6	2.1±0.7	4.8±1.0	3.6±0.8
B	10.8±3.0	2.0±0.5	6.2±0.9	4.5±0.7	5.0±0.8	13.5±1.5	2.8±0.4
C	7.9±1.5	2.3±0.6	1.6±0.4	1.5±0.4	1.4±0.7	2.4±0.6	0.8±0.4
D	0	0.1±0.1	0.3±0.2	0	0.3±0.3	0.3±0.2	0.1±0.1
E	0.5±0.3	0.2±0.1	0.1±0.1	0	0	0.3±0.2	0.1±0.1
F	0.5±0.3	0.1±0.1	0.1±0.1	0	0.2±0.2	0	0
	Diplura						
A	0.3±0.2	0.2±0.1	0.2±0.2	0	0.2±0.1	0	0
B	0.3±0.2	0.2±0.1	0.1±0.1	0	0.2±0.1	0.3±0.2	0
C	0.6±0.3	0.1±0.1	0	0	0	0.3±0.2	0
D	0	0.1±0.1	0	0	0	0	0
E	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0

APPENDIX B. Numbers of small soil animals extracted with Baermann funnels. No./25 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 15 and 16 May, 1974.

1974	11MAY	20MAY	1JUNE	15JUNE	15JULY	19SEPT.	6DEC.
	Enchytraeidae						
A	5.2±0.8	1.2±0.4	2.7±0.8	0.6±0.2	2.1±0.6	0.9±0.3	0
B	5.2±0.8	2.7±0.7	2.2±0.5	1.8±0.7	4.0±0.9	0.9±0.6	0
C	3.2±1.0	1.3±0.6	0.7±0.3	0.8±0.4	0.1±0.1	0.2±0.1	0
D	4.4±0.8	3.4±0.5	4.5±0.7	7.2±2.7	8.8±1.4	2.3±0.4	0.3±0.2
E	3.9±1.1	1.6±0.7	1.6±0.5	2.8±0.7	1.5±0.4	3.2±1.3	0.1±0.1
F	3.9±1.1	1.4±0.8	1.1±0.5	4.1±1.5	3.8±1.1	5.7±1.4	1.3±0.4
	Nematoda						
A	39.2±8.4	114±14.0	44.8±7.3	45.3±4.0	32.7±4.4	84.6±14.7	151±22.7
B	39.2±8.4	65.8±6.9	49.5±6.2	50.6±6.5	39.7±4.3	228±39.5	194±19.1
C	53.2±9.4	77.6±10.6	51.9±9.4	31.7±6.8	13.8±5.1	21.2±4.7	49.6±19.6
D	31.5±4.4	46.1±9.4	63.1±10.8	31.0±2.4	20.4±2.8	42.8±5.2	110±10.4
E	24.2±4.5	95.7±13.4	28.0±5.0	14.9±4.0	15.7±2.4	621±23.1	525±13.1
F	24.2±4.5	23.0±4.2	74.6±20.1	29.9±5.2	44.2±6.1	54.7±8.2	126±14.3
	Rotifera						
A	1.5±0.4	2.7±0.7	1.2±0.4	0.2±0.1	0	0.9±0.3	2.6±0.8
B	1.5±0.4	1.0±0.3	1.5±0.7	0.1±0.1	0.3±0.2	3.6±1.1	6.2±1.2
C	0.1±0.1	0.1±0.1	0	0	0	0	0.1±0.1
D	0.2±0.1	1.9±0.7	1.9±0.6	0.3±0.2	0.2±0.1	2.8±0.7	6.1±1.0
E	1.6±0.9	0.2±0.1	0.4±0.3	0	0	0.3±0.2	0.1±0.1
F	1.6±0.9	0	0.4±0.2	0	0	0.6±0.3	2.6±1.3
	Tardigrada						
A	0	0	0.1±0.1	0.2±0.1	0	0.2±0.1	0
B	0	0	0.1±0.1	0.4±0.2	0	0	0
C	0	0	0.2±0.1	0.8±0.3	0	0	0.1±0.1
D	0	0	0.1±0.1	0	0	0	0
E	0	0	0	0	0	0	0
F	0	0	0.3±0.2	0	0	0.1±0.1	0

APPENDIX C. Numbers of small soil animals extracted with Tullgren funnels. No./100 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 7 May, 1975.

1975	2 MAY	12 MAY	9 JUNE	21 JULY	3 SEPT.	2 NOV.
	Collembola					
A	4.2±0.4	1.6±0.5	3.0±1.1	0.6±0.2	0	4.0±0.7
B	7.6±2.1	13.4±3.1	7.2±1.1	2.8±1.0	0	15.2±2.6
C	1.6±0.5	0.2±0.2	0.2±0.2	0	0	7.2±3.2
D	2.6±0.7	1.0±0.6	1.4±0.5	1.8±0.8	0	12.6±1.6
E	0.6±0.4	1.0±0.3	0.4±0.4	0.2±0.2	0.2±0.2	1.4±0.5
F	7.0±1.0	1.2±0.2	4.6±0.6	1.4±0.6	0.6±0.4	7.0±1.3
	Cryptostigmata					
A	7.2±1.4	10.0±0.9	5.4±0.7	1.2±0.4	0.6±0.6	17.0±3.2
B	12.4±0.8	13.8±0.7	6.8±1.9	3.6±1.0	0	12.8±1.6
C	1.2±0.2	0	0.2±0.2	0.8±0.6	0	0.8±0.4
D	0	0	0	0	0	3.2±0.7
E	0	0.2±0.2	0	0	0	0
F	0	0.2±0.2	0	0	0	0
	Other Acari					
A	2.6±1.1	6.4±0.8	3.4±1.5	1.2±0.6	4.4±1.5	3.2±0.6
B	6.8±0.8	17.4±3.1	11.4±2.4	9.4±2.0	1.0±0.3	3.8±0.9
C	2.2±0.8	3.2±0.9	1.0±0.6	0.6±0.2	0	0.8±0.4
D	0.6±0.4	0.8±0.4	1.2±0.4	1.6±0.7	3.2±0.4	3.8±1.6
E	0	0.2±0.2	0	0.4±0.2	0	0
F	1.2±0.4	0	0	0.2±0.2	2.0±0.6	0.2±0.2
	Diplura					
A	0	0.2±0.2	0	0	0	0
B	0.8±0.6	0.2±0.2	0.2±0.2	0	0	0
C	0.2±0.2	0	0	0	0	0
D	0	0	0	0	0	0
E	0	0	0	0	0	0
F	0	0	0	0	0	0

APPENDIX D. Numbers of small soil animals extracted with Baermann funnels. No./25 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 7 May, 1975.

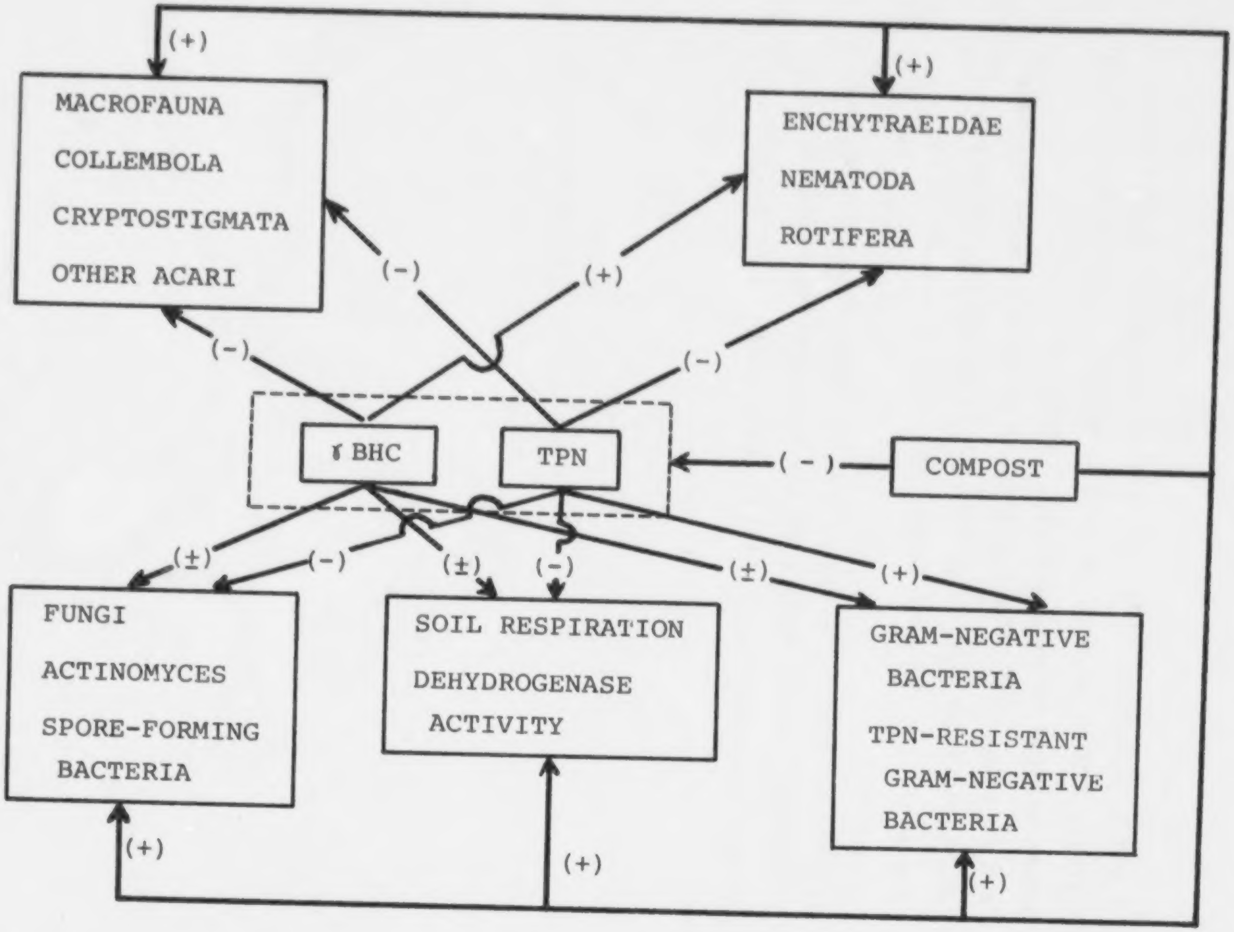
1975	2MAY	12MAY	9JUNE	21JULY	3SEPT.	2NOV.
	Enchytraeidae					
A	0	0.4±0.2	0.6±0.4	0	0	0
B	0.2±0.2	0.2±0.2	2.0±0.6	0.4±0.4	0	0.8±0.4
C	0	0	0	0	0	0
D	0.4±0.2	0.2±0.2	1.0±0.8	0	0	0.2±0.2
E	0	0	0.2±0.2	0	0	0
F	1.0±0.0	0.2±0.2	1.8±0.6	0	0	0.4±0.2
	Nematoda					
A	183±19.7	114±27.7	91.6±3.4	119±11.7	29.2±2.2	203±9.4
B	322±40.4	321±29.1	376±22.6	399±23.5	183±18.1	478±53.5
C	124±8.6	144±22.0	70.6±12.9	23.2±1.4	3.4±0.4	32.2±4.4
D	181±27.0	155±18.7	79.0±10.5	178±8.7	76.0±6.1	109±14.1
E	36.4±4.0	47.8±8.5	54.6±7.7	806±5.5	15.0±4.4	95.0±5.8
F	214±13.8	172±22.3	162±12.7	593±32.4	337±24.2	334±5.2
	Rotifera					
A	1.3±0.6	2.0±0.7	4.0±1.1	0.8±0.5	0.4±0.4	3.8±1.5
B	1.4±0.5	3.0±0.6	9.0±0.6	5.4±0.9	0.8±0.4	7.0±1.5
C	0.2±0.2	0	0.2±0.2	0.2±0.2	0	0
D	2.0±0.6	3.0±1.3	3.4±0.8	2.6±0.4	0.4±0.2	2.8±0.8
E	0.2±0.2	0	0.2±0.2	0	0	3.2±2.7
F	0.6±0.2	0.6±0.4	0	0	0	2.2±1.0
	Tardigrada					
A	0	0	0	0	0	0.2±0.2
B	0	0	0	0	0	0
C	0	0	0.4±0.2	0	0	0
D	0	0	0	0	0.2±0.2	0
E	0	0	0	0	0	0
F	0	0	0	0	0	0

APPENDIX E. Numbers of small soil animals extracted with Tullgren funnels. No./100 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 15 May. 1976.

1976	10 MAY	20 MAY	15 JUNE	21 JULY	12 NOV.
	Collembola				
A	23.0±2.6	6.4±1.5	23.2±4.2	6.4±1.3	6.0±0.6
B	26.0±1.3	8.0±1.7	16.8±2.2	17.4±2.3	31.5±4.0
C	14.6±1.0	0.8±0.4	0.4±0.2	1.2±0.8	17.2±3.8
D	65.2±3.6	3.6±0.9	8.2±0.9	4.2±1.6	18.2±2.9
E	13.4±1.0	0.2±0.2	0.4±0.4	0.2±0.2	3.8±0.7
F	10.2+1.4	0.2±0.2	0.2±0.2	1.4±0.8	11.0±1.2
	Cryptostigmata				
A	66.0±11.4	26.4±3.8	76.4±10.5	8.0±1.7	18.4±3.2
B	35.2±4.1	26.0±2.9	60.0±6.4	24.6±1.7	25.0±3.0
C	6.0±2.0	1.8±0.6	1.0±0.3	0	0.2±0.2
D	6.8±1.5	0.4±0.4	5.0±0.9	2.2±0.9	2.8±0.6
E	0	0	1.0±0.6	0.2±0.2	0
F	1.2±0.4	0	0.8±0.6	0	0.3±0.3
	Other Acari				
A	8.2±0.5	2.2±0.2	21.2±3.2	2.0±0.3	12.4±1.1
B	6.4±1.2	8.4±1.1	38.0±9.6	8.4±5.7	14.5±1.3
C	5.8±3.4	1.0±0.5	1.8±0.5	0.8±0.8	1.4±0.7
D	1.8±0.5	0.8±0.4	0.4±0.4	0.4±0.2	4.0±0.9
E	1.0±0.5	0	2.0±0.8	0	1.4±0.9
F	1.8±0.6	0.4±0.2	0.8±0.4	0	0.8±0.3
	Diplura				
A	0.2±0.2	0.2±0.2	0	0	0
B	0.2±0.2	0	0	0	0
C	0	0	0	0	0
D	0.2±0.2	0	0	0	0
E	0	0	0	0	0
F	0	0	0	0	0

APPENDIX F. Numbers of small soil animals extracted with Baermann funnels. No./25 cm^3 with S.E. Compost, fungicide and insecticide were supplied on 15 May, 1976.

1976	10 MAY	20 MAY	15 JUNE	21 JULY	12 NOV.
	Enchytraeidae				
A	0.8±0.5	1.0±0.5	1.8±0.7	0.4±0.2	0.2±0.2
B	3.0±1.0	2.2±0.6	21.8±2.8	4.0±0.6	0.6±0.2
C	1.0±0.5	0	0	0	0.6±0.4
D	0.8±0.5	2.2±1.5	8.0±1.4	1.8±0.4	0.6±0.4
E	1.0±0.6	0	0.2±0.2	0	0.2±0.2
F	0.4±0.2	0	0.2±0.2	0.4±0.2	2.2±0.5
	Nematoda				
A	216±41.2	189±29.8	401±19.1	169±23.8	436±33.9
B	357±71.2	366±24.4	720±54.3	497±21.1	303±38.8
C	170±14.5	92.0±8.6	108±17.1	40.2±6.3	64.4±8.6
D	300±23.9	155±6.0	185±11.9	89.4±6.4	166±5.5
E	153±8.3	54.0±4.5	56.2±5.5	18.0±1.0	68.2±7.0
F	324±29.7	125±5.8	270±9.9	121±10.5	207±20.7
	Rotifera				
A	4.5±1.8	2.8±0.9	2.8±1.5	5.0±1.2	3.6±1.3
B	11.8±2.2	22.6±4.2	28.2±4.3	19.8±5.3	15.4±3.0
C	1.0±0.8	2.6±1.8	0.8±0.6	6.0±3.2	1.2±0.6
D	2.6±0.6	5.4±0.8	10.2±3.0	6.0±1.3	6.2±1.2
E	0.2±0.2	0.4±0.4	4.6±3.7	3.4±2.9	0.2±0.2
F	1.8±0.5	2.0±1.8	2.0±1.3	0.2±0.2	2.4±0.5
	Tardigrada				
A	0	0	0	0	0
B	0	0	0	0	0.4±0.2
C	0.2±0.2	0	0	0	0
D	0.2±0.2	0	0	0	0
E	0	0	0	0	0
F	0	0	0	0	0


(+)
(+)
MACROFAUNA
COLLEMBOLA
CRYPTOSTIGMATA
OTHER ACARI
ENCHYTRAEIDAE
NEMATODA
ROTIFERA
(-)
(+)
(-)
(-)
γ BHC
TPN
(-)
COMPOST
(±)
(-)
(±)
(-)
(±)
(+)
FUNGI
ACTINOMYCES
SPORE-FORMING BACTERIA
SOIL RESPIRATION
DEHYDROGENASE ACTIVITY
GRAM-NEGATIVE BACTERIA
TPN-RESISTANT GRAM-NEGATIVE BACTERIA
(+)
(+)
(+)

(+) ACCERELATE· INCREASE (-) INHIBIT· REDUCE

(±) (+) OR (-)· NO INFLUENCE

FIGURE 1. The relations among effects of compost, TPN and γ BHC on numbers of soil fauna, soil microbes, rates of soil respiration and dehydrogenase activity in the soil. (Kitazawa, Yang, Wada, Takai 1975. From Takai 1977)

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EFFECT OF TWO HERBICIDES ON THE SOIL INHABITING CRYPTOSTIGMATID MITES

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INTRODUCTION

Herbicides administered for the elimination of unwanted plants in the agroecosystems may unintentionally upset the balance of the ecosystem by affecting the sensitive nontarget soil animals like cryptostigmatid mites. Effects of these chemicals on the soil fauna have been recently reviewed by Rijsackers and ver der Drift (1976). Notwithstanding this, very little information is available to date regarding the influence of weedicides on the nontarget fauna of the soil in tropical countries like India. Here the use of these chemicals is gaining momentum, with the development of modern agrotechnical measures following a "grow more food" campaign. This communication deals with the possible ill effects of two herbicides, Nitrofen (2,4 - dichlorophenyl - 4 - nitrophenyl ether) and Propanil (3,4 - dichloropropion anilide), which are of very common use in India, on the community structure, species diversity and density of cryptostigmatid mites, under field and laboratory conditions.

MATERIAL AND METHODS

A rabi crop (early October to February) of a dry cultivatable variety of paddy, "Pusa - 2-21", was raised for the experimental purposes in three small highland plots with laterite soil. All the normal agricultural manipulations were employed simultaneously in the plots except for the application of herbicides in the two treated plots. Single applications of the herbicides, Nitrofen (Tok, E-25) and Propanil (Stam, F-34), were made in the lowest agricultural doses recommended for general weed control in paddy crops in India by Mukhopadhyay and Bhattacharyay (1967). Nitrofen at the rate of 2 kg' ai/ha was sprayed as a pre-emergence herbicide, while Propanil was used for post-emergence weed control at the rate of 3 kg. ai/ha. Details regarding the maintenance of the crop, soil samplings, extraction and identification of the fauna are being published elsewhere (Bhattacharya and Joy, in press). The field experiment was conducted from the month of September 1977 to February 1978, and soil samples were collected at fortnightly intervals.

Analysis of the data obtained from the field experiment were made with respect to the relative abundance and frequency after Dindal (1977), and density and species diversity of cryptostigmatid community. The latter was compared with the help of Shannon and Weaver index (Shannon and Weaver, 1963). A comparison of the cryptostigmatid density as a whole and of the dominant species (frequency > 50%), between the treated and untreated plots was made and their statistical significance was checked with the help of 'tw' test (Lord, Pages 120-122, quoted in Snedacor and Cochran, 1947). Percentile deviation of the density of these groups in the treated plots, in relation to that of the untreated plot was also estimated.

The dominant species encountered in the field experiment were subjected to the same doses of the two herbicides under laboratory conditions. A known number of live cryptostigmatid mites of the same age group and size, reared for the purpose under laboratry conditions, was placed in special treatment cells containing sterile soil sprayed with the herbicide solution. Details of the rearing techniques are given elsewhere (Bhattacharya, Joy and Joy, 1978). Untreated control cells were also maintained in the laboratory and the mortality of the mites in both the sets was estimated after 7 days.

RESULTS

Field experiment

The overall density of all the cryptostigmatid species collected from the untreated (UT), Nitrofen treated (T_1) and Propanil treated (T_2) plots is given in Figure 1. In all, 11 species were encountered in the UT plot while there were nine each in the T_1 and T_2 plots.

Relative Abundance and Frequency

Scheloribates albialatus and *Oppia nodosa* were the two dominant species in all the plots (Table 1). Their dominance was more prominent in the treated plots prior the the herbicide applications. Figure 2 shows the degree of response by different cryptostigmatid species to the herbicide. Both *S. albialatus* and *O. nodosa* became subdominants after Nitrofen application while only *S. albialatus* lost its dominant status as a result of Propanil treatment. *Paroppia* sp. and *Archegozetes longisetosus* which were subdominants in the T_1 plot became occasional and rare respectively, while *Galumna* sp. and *Cosmochthonius emmae* remained unaffected. In the T_2 plot most of the species remained unaltered in their status after the herbicide treatment.

Species Diversity

The analysis of the cryptostigmatid community according to the Shannon and Weaver index (Table 2) shows that there is no significant change in the species diversity after the application of Nitrofen (t=0.198), while the Propanil treatment signifantly shifted the diversity of species (t=4.52, $P < 0.05$).

Table 2: A COMPARISON BETWEEN THE SPECIES DIVERSITY OF CRYPTOSTIGMATID COMMUNITY BEFORE AND AFTER THE HERBICIDE TREATMENT.

HERBICIDE	N	S	H'	±	S. E.
NITROFEN					
Pre-treatment	100	8	1.66956	±	0.0682
Post-treatment	96	7	1.65517	±	0.0613
PROPANIL					
Pre-treatment	111	9	1.82685	+	0.0692
Post-treatment	161	8	1.40540	±	0.067

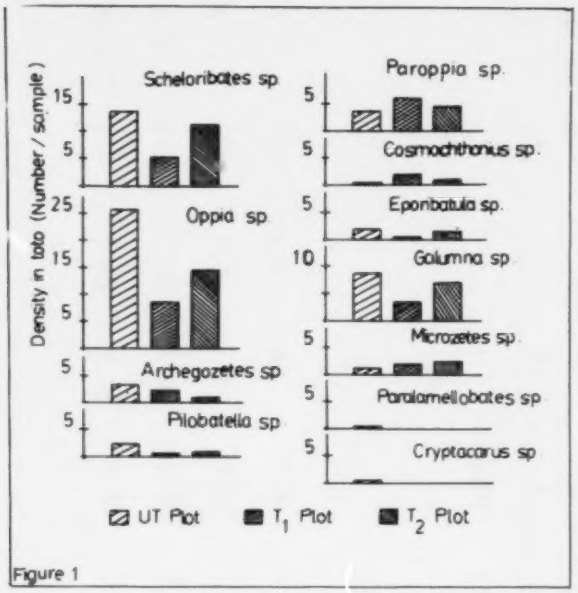

Figure 1. OVERALL POPULATION DENSITY OF THE DIFFERENT CRYPTOSTIGMATID SPECIES IN THE EXPERIMENTAL PLOTS.

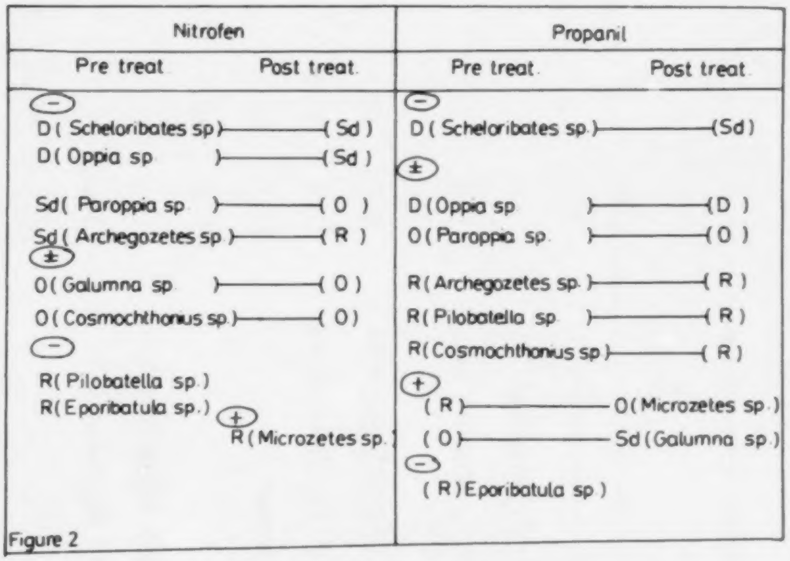
Nitrofen
Pre treat
Post treat
−
D (Scheloribates sp) —— (Sd)
D (Oppia sp) —— (Sd)
Sd (Paroppia sp) —— (O)
Sd (Archegozetes sp) —— (R)
±
O (Galumna sp) —— (O)
O (Cosmochthonius sp) —— (O)
−
R (Pilobatella sp.)
R (Eporibatula sp.)
+
R (Microzetes sp.)
Propanil
Pre treat
Post treat
−
D (Scheloribates sp) —— (Sd)
±
D (Oppia sp) —— (D)
O (Paroppia sp) —— (O)
R (Archegozetes sp) —— (R)
R (Pilobatella sp) —— (R)
R (Cosmochthonius sp) —— (R)
+
(R) —— O (Microzetes sp.)
(O) —— Sd (Galumna sp.)
−
(R) Eporibatula sp.)
Figure 2

Figure 2. RESPONSES OF THE DIFFERENT CRYPTOSTIGMATID SPECIES TO THE HERBICIDE APPLICATION IN THE TREATED PLOTS.

Table 1: RELATIVE ABUNDANCE AND FREQUENCY OF THE CRYPTOSTIGMATID SPECIES IN THE EXPERIMENTAL PLOTS

SPECIES	UT		T_1				T_2			
			Pre-treat.		Post-treat.		Pre-treat.		Post-treat.	
	RA	F	RA	F	RA	F	RA	F	RA	F
Cosmochthonius emmae Berlese	0.5	3.5	5.0	20.0	7.3	10.6	3.6	9.5	1.2	5.1
Cryptacarus dendrisetosus Bhattacharya, Bhaduri and Raychaudhuri	0.3	1.7	-	-	-	-	-	-	-	-
Archegozetes longisetosus Aoki	6.2	13.8	13.0	46.7	1.0	2.1	3.6	6.7	0.6	2.6
Microzetes auxillaris Grandjean	1.9	12.1	-	-	12.5	17.0	3.6	6.7	6.2	18.0
Oppia nodosa Hammer	41.4	48.3	33.0	73.3	28.1	36.2	18.9	66.7	46.0	71.8
Paroppia sp.	6.4	13.8	12.0	40.0	30.2	17.0	17.1	23.8	4.4	12.8
Paralamellobates bengalensis Bhaduri and Raychaudhuri	0.3	1.7	-	-	-	-	-	-	-	-
Galumna sp.	13.9	40.0	10.0	26.7	10.4	11.9	12.6	10.0	18.6	38.5
Eportibatula sp.	2.7	5.2	1.0	6.7	-	-	7.2	6.7	-	-
Scheloribates albialatus Hammer	23.0	62.1	25.0	66.7	10.4	38.3	31.5	76.2	22.4	46.2
Pilobatella sp.	3.5	6.9	1.0	6.7	-	-	1.8	9.5	0.6	2.6

RA = Relative abundance: > 40% Dominant
10 to 40% Subdominant
< 10% Rare

F = Frequency: > 50% Dominant
30 to 50% Subdominant
10 to 30% Occasional
< 10% Rare

N = Number of Individuals
S = Number of Species
H'= Shannon and Weaver Index in log e

Comparison Between the Densities

The fluctuation in the densities of cryptostigmatid population as a whole and of the two dominant species under consideration (frequency > 50%), in the three plots at various intervals of sampling are given in Figure 3. Table 3 shows that both Nitrofen and Propanil significantly decreased the density of cryptostigmatid mites as a whole after their application.

Table 3: Values of 'tw' test between different intervals of sampling in the experimental plots.

SAMPLING OCCASIONS	CRYPTOSTIGMATA		
	UT tw	T_1 tw	T_2 tw
I vs. II	0.285	0.222	0.688 ***
II vs. III	0.207	→ 0.395 *	0.045
III vs. IV	0.117	0.222	→ 0.420 **
IV vs. V	0.225	0.149	0.271
V vs. VI	0.123	0.143	0.261
VI vs. VII	0.354 *	0.157	0.148
VII vs. VIII	0.222	0.096	0.123
VIII vs. IX	0.393 *	0.372 *	0.571 ***

* $P < 0.05$
** $P < 0.02$
*** $P < 0.01$

The arrows indicate the stage at which herbicide was treated

Turning to the dominant species, it was noted that both the herbicides depressed the population levels of S. albialatus and O. nodosa on their application (Table 4). However, the effect was more drastic and statistically significant in the case of Nitrofen, for both the species.

Table 4: A comparison between the densities of the two dominant species of Cryptostigmata in Untreated and Treated plots after the herbicide application.

SPECIES	No./Sample			No./Sample		
	UT	T_1	tw	UT	T_2	tw
Scheloribates albialatus	7.6	1.4	0.614 ***	7.3	6.0	0.121
Oppia nodosa	19.3	3.9	0.441 **	21.0	12.3	0.231

** $P < 0.02$ *** $P < 0.01$

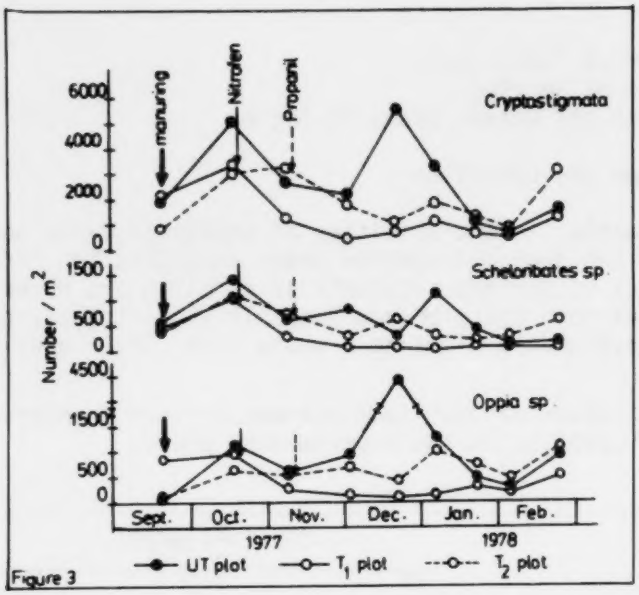

Figure 3. CHANGES IN THE DENSITY OF THE TOTAL CRYPTOSTIGMATID MITES AND OF THE TWO DOMINANT SPECIES.

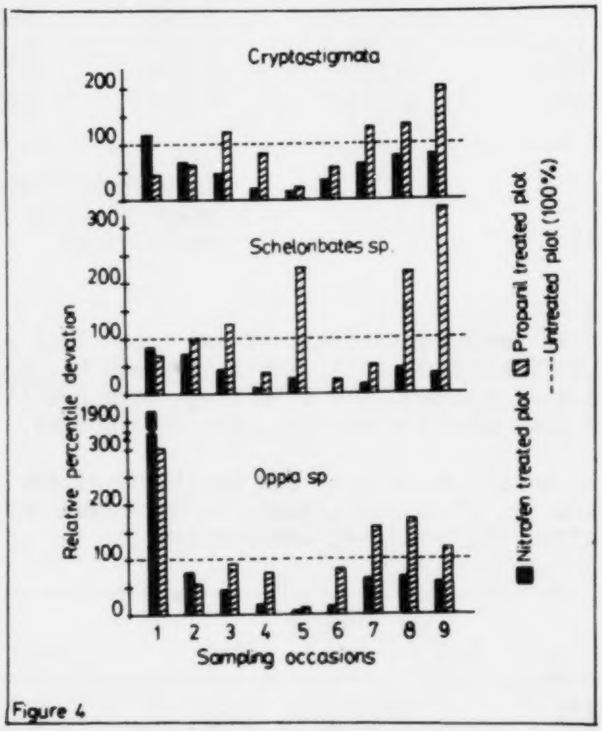

Figure 4. RELATIVE PERCENTILE DEVIATIONS IN THE DENSITY OF THE TOTAL CRYPTOSTIGMATID MITES AND OF THE TWO DOMINANT SPECIES IN THE TWO TREATED PLOTS IN RELATION TO THE UNTREATED PLOT

An analysis of the percentile deviations of the densities of Cryptostigmata in toto and of the two dominant species in the two treated plots, in relation to those of the untreated plot at various intervals of sampling (Figure 4) also indicated that Nitrofen has more adverse effect on the nontarget organisms under field conditions.

Laboratory experiment

Results of the experiment conducted in the laboratory (Table 5) revealed that the agricultural dose of Nitrofen killed all the individuals of S. albialatus and O. nodosa within 7 days, while that of Propanil killed all the specimens of O. nodosa; about 6.5% of the total S. albialatus were still alive within that period. On the other hand, in the untreated control cells all the individuals of S. albialatus and O. nodosa remained active after 7 days and many of these cells contained newly laid eggs.

Table 5: EFFECT OF THE AGRICULTURAL DOSES OF HERBICIDES ON TWO SPECIES OF CRYPTOSTIGMATID MITES UNDER LABORATORY CONDITIONS.

SPECIES	R	N	UT			R	N	T_1			R	N	T2		
			A	I	D			A	I	D			A	I	D
O. nodosa	20	250	250	-	-	18	180	-	-	180	18	180	-	-	180
S. albialatus	18	220	220	-	-	20	200	-	-	200	20	200	-	13	187

UT - Untreated control cells
T_1 - Nitrofen treated cells
T_2 - Propanil treated cells

R - Replications
N - Number of Individuals
A - Active
I - Inactive
D - Dead

DISCUSSION

Findings of this investigation indicate that the single dose application of Nitrofen and Propanil can affect the density and diversity of cryptostigmatid mites in a paddy field. Experimental evidences further suggest that these herbicides have a direct killing action at least on the two species under consideration. Adverse effect of herbicides like Shell WL 19805, Paraquat, 2,4-D and Simazine, on the soil inhabiting cryptostigmatid mites has also been shown by Edwards (1970), Edwards and Lofty (1975) and Prasse (1975). Edwards (1970) showed that the Sehll WL 19805 had less adverse effect on the cryptostigmatid mites when the plots were rotovated after spraying, than in plots with the herbicide left on the soil surface. It is known in the case of Nitrofen, that it should not be incorporated in soil but placed as a thin layer on the soil surface (Brian, 1976) and that the herbicidal activity of this chemical is rapidly lost if incorporated with the soil

(Mukhopadhyay, 1972). Edwards and Lofty (1975) while comparing the density of cryptostigmata in Paraquat treated, direct drilled plots with those in ploughed ones, said that the former has less impact on the number of soil animals. Similarly Prasse (1975) observed that the herbicide Simazine significantly decreased the number of the cryptostigmatid mite, Tectocepheus velatus (Michael) in up to 10 cms of soil, while 2,4-D could not produce any significant decline. It seems that both ploughing and herbicide application done in the same plot can decrease the population of nontarget organisms of soil.

CONCLUSION

It may be concluded that the herbicide Nitrofen had more adverse effect on the cryptostigmatid mites compared to Propanil in field conditions. Experimental evidences under laboratory conditions suggest that these weedicides have a direct knock-down effect at least on cryptostigmatid mites like O. nodosa and S. albialatus.

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SESSION II: HUMAN WASTE DISPOSAL AND SOIL ORGANISMS

Moderator: K. H. Domsch

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BIOLOGICAL SUCCESSION IN ARTIFICIAL SOIL MADE OF SEWAGE SLUDGE AND CRUSHED BARK

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The present paper summarizes the main results of a 3-year study dealing with the biological processes that occur during the humification of municipal sewage sludge, with particular reference to the use of sludge as artificial soil in environmental building. The types of sludge used for the experiments were 1) digested sludge from a biological-chemical plant (activated sludge process with Fe_2SO_4 precipitation), 2) activated sludge (=1 without digestion, but lime and ferric chloride added), and 3) limed sludge from a chemical plant (lime content ca. 50 % of dry matter). These were dried to ca 20 % dry matter content and mixed 1 to 1 (vol) with crushed pine or spruce bark. The test plots were established on a small parcel of field from which the topsoil had been removed. The materials were applied in squares ca 25 cm deep and 14 m^2 in area.

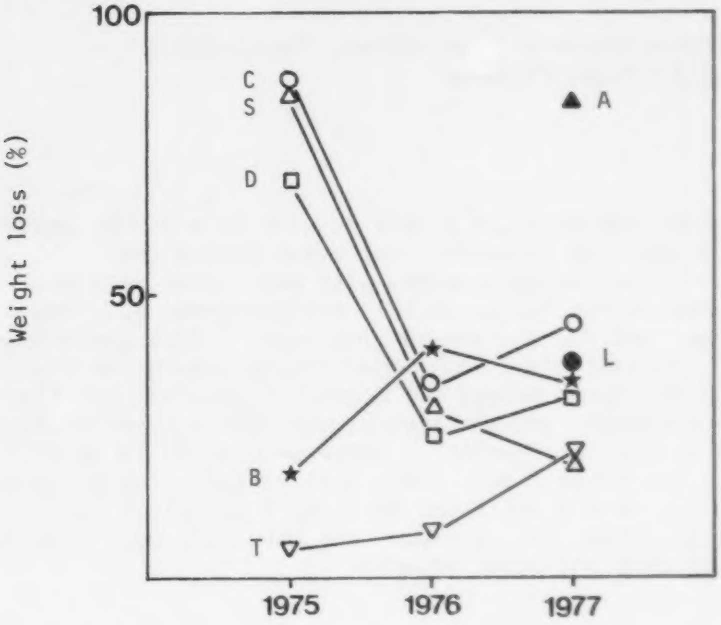
The principal study objects were: 1) uncomposted digested sludge and bark, 2) uncomposted activated sludge and bark, 3) uncomposted limed sludge and bark, and 4) digested sludge and bark after 1 year's composting. These were compared with 5) digested sludge alone, 6) crushed bark alone, 7) compost made of digested sludge and bark, 8) cultivated field soil, 9) garden grassland soil, and 10) forest soil.

The variables measured were: physical and chemical properties of the test materials, contents of heavy metals in soil and vegetation, production of the vegetation, total numbers of bacteria, numbers of Clostridia, Streptomycetes, Protozoa, and glucose-fermenting bacteria, length of fungal hyphae (Sundman & Sivelä, 1978), numbers of specific groups of microbes indicating the nitrogen metabolism and hygienic state of the materials, nitrification and dehydrogenase activity, oxygen consumption, cellulose degradation, numbers and biomasses of groups and species of invertebrates, total animal biomass and changes in the animal communities.

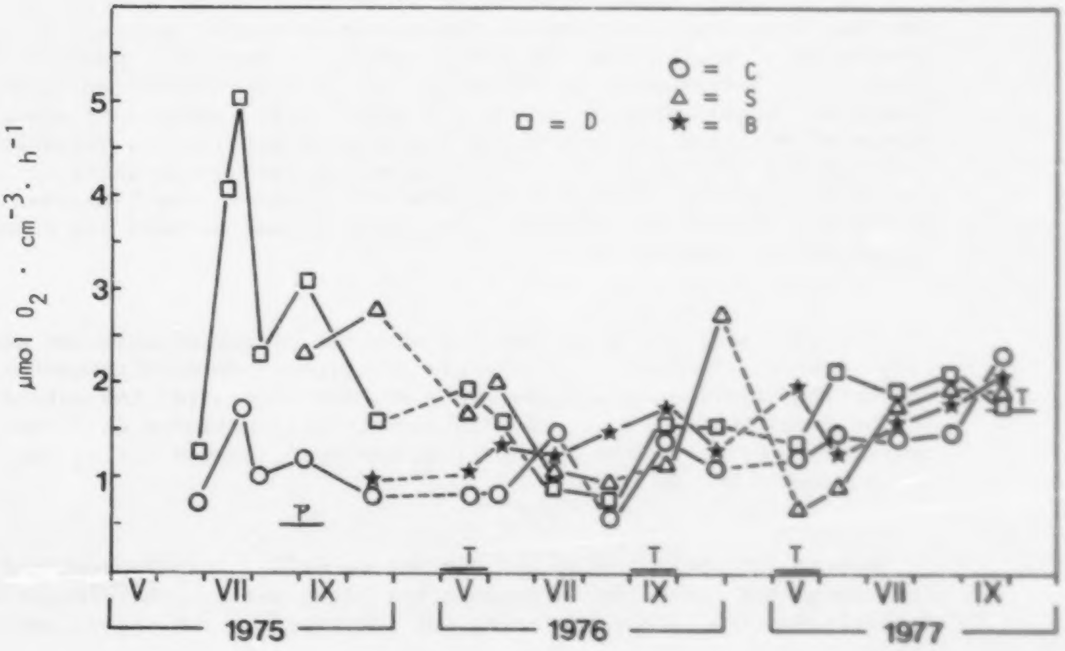
In fresh mixtures of sludge and bark the microbial activity was very intense. Numbers of clostridia and glucose-fermenting bacteria, indicating anaerobic processes, were highest soon after the establishment of the experimental plots. Biological activity, measured as oxygen consumption or cellulose degradation, was most intense during the first growing period (Figure 1).

Numbers of denitrifying and nitrate-reducing bacteria remained high in uncomposted materials throughout the study period. Nitrification activity was low in the beginning but increased in the second and third years.

FIGURE 1. Degradation of cellulose in 90-day periods (top), and consumption of oxygen (bottom) in the different materials tested. Symbols used:



D = uncomposted mixture of digested sludge and bark,
A = " " " activated sludge and bark,
L = " " " limed sludge and bark,
C = composted mixture of digested sludge and bark,
S = digested sludge alone,
B = bark alone,
T = tillage used as reference.



Flying insects (Coleoptera and Diptera), and phoretic nematodes and mites (Mesostigmata, Prostigmata, Astigmata) transported by them colonized fresh mixtures of sludge and bark in a few days and reproduced rapidly. These early groups became less numerous as the materials aged. Collembola propagated dense populations within a few weeks and retained an important position through all stages, while Oribatei were among the late colonists (Figure 2).

The animal community during the early stages of succession can be described as typical for dung and related accumulations of easily decomposable organic matter. This "dung community" changes relatively rapidly into a less specialized "compost community", and gradually further into a community of generalist soil dwellers (Figure 3). However, even in the oldest material tested, a composted mixture of digested sludge and bark in the third year after application, the animal community differed considerably from that of the adjacent arable soil.

Of the fresh mixtures examined, that of activated sludge and bark showed the highest biological activity and harbored the greatest animal biomass. The mixture of digested sludge showed the lowest activity and biomass, and that of limed sludge took an intermediary position (Figure 4). Enchytraeidae and Lumbricidae were almost absent during the first year in the mixtures containing digested and limed sludges, while Enchytraeidae were especially numerous in that with activated sludge. Digested and limed sludges were obviously harmful or toxic to these groups, a fact verified for earthworms by culture experiments.

Composting strongly promoted the biological processes in the materials tested. After one year's composting the mixture of digested sludge and bark attained a degree of stability which was not achieved by the uncomposted mixture even in the third growing season. High nitrification activity characterized the composted mixture in comparison with the uncomposted ones.

In the mixtures of digested sludge and bark the processes proceeded more rapidly than in either of the component materials alone. Bark alone differed from the sludge materials in its biological properties: fungal hyphae were especially abundant (Figure 5), and the animal community contained some characteristic species, the Enchytraeidae dominating in the faunal biomass.

In addition to the composting, freezing in winter was shown to improve the hygienic state of the sludge-containing materials: numbers of fecal coliforms, which remained high through the first growing season, had dropped to practically zero by the next summer (Figure 6). Fecal streptococci, on the other hand, were not affected by low winter temperatures.

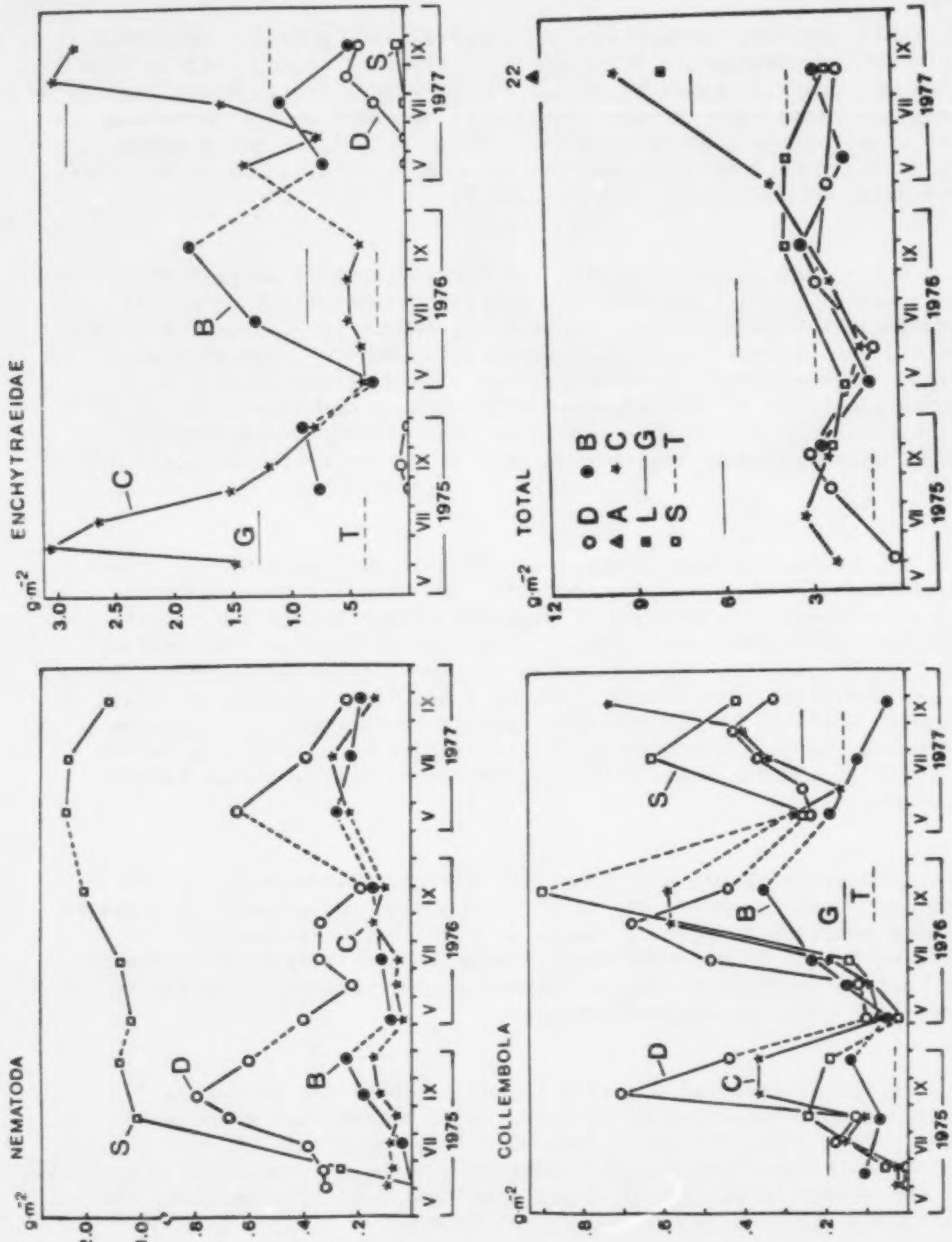
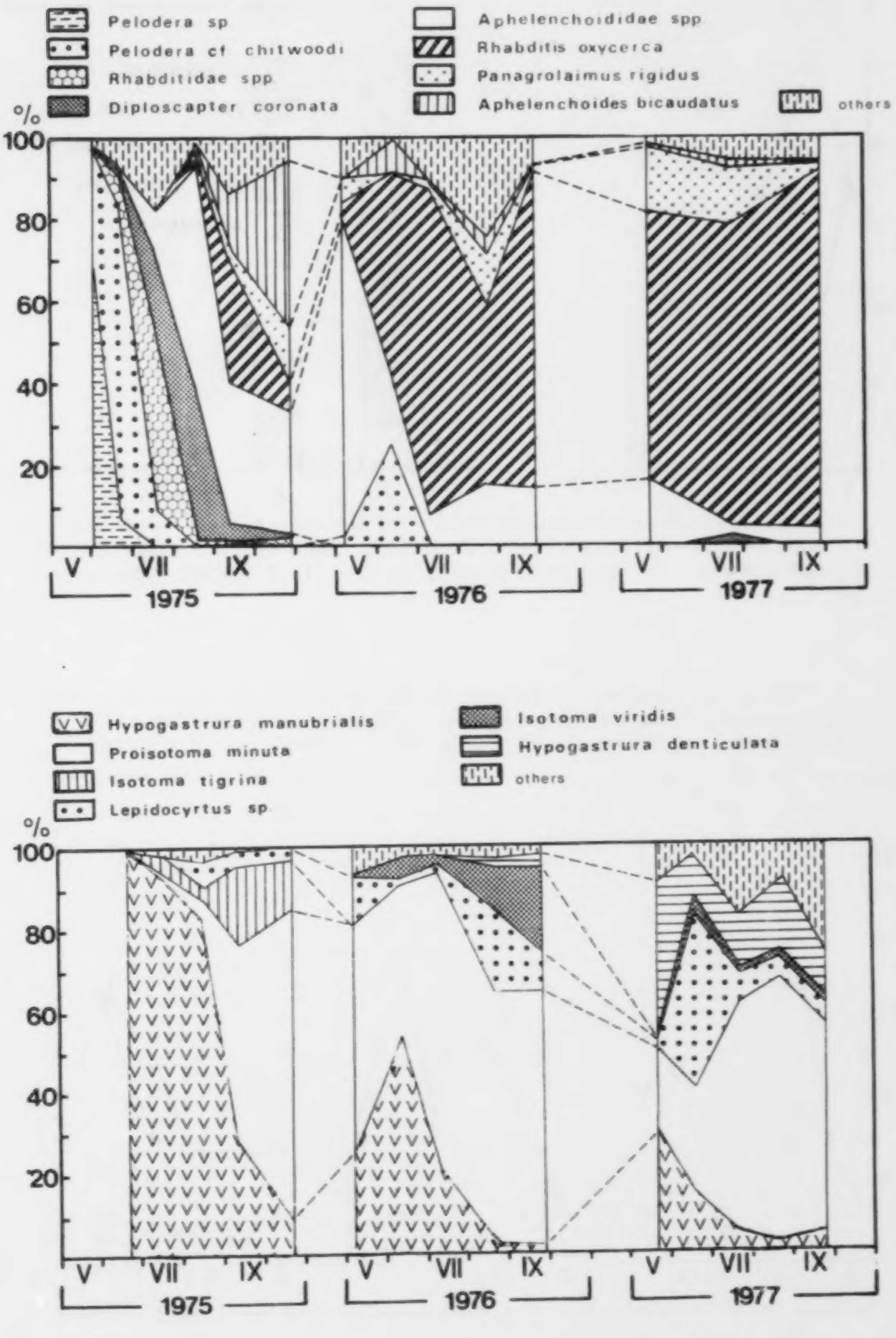


FIGURE 2. Biomasses of Nematoda, Enchytraeidae and Collembola, and total animal biomass in the different materials tested. Average annual levels in the reference soils indicated by horizontal lines. G = garden grassland; other symbols as in Figure 1.

FIGURE 3. Changes in the communities of Nematoda (top) and Collembola in an uncomposted mixture of digested sludge and bark (relative abundances).



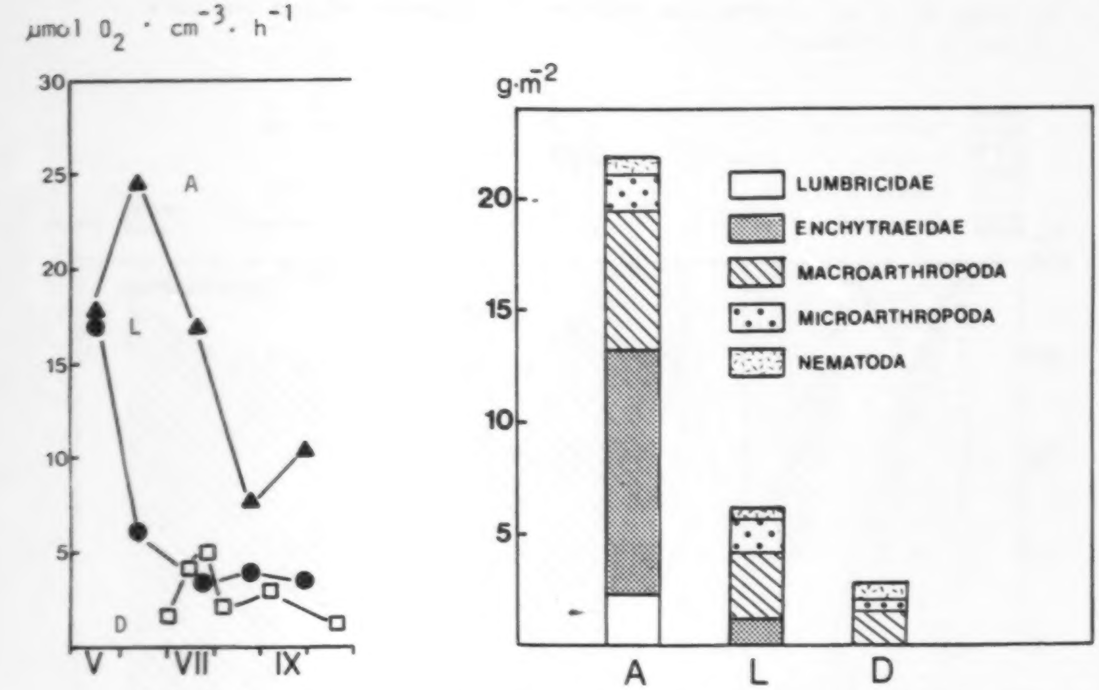


FIGURE 4. Oxygen consumption (left) and average animal biomasses in uncomposted mixtures of activated (A), limed (L) and digested (D) sludge and bark in the first growing period (1975 for D, 1977 for A and L).

FIGURE 5. Lengths of fungal hyphae in different materials tested. For methodical reasons the data for 1975 are not quantitatively comparable with those for 1976 and 1977. Symbols as in Figure 1.

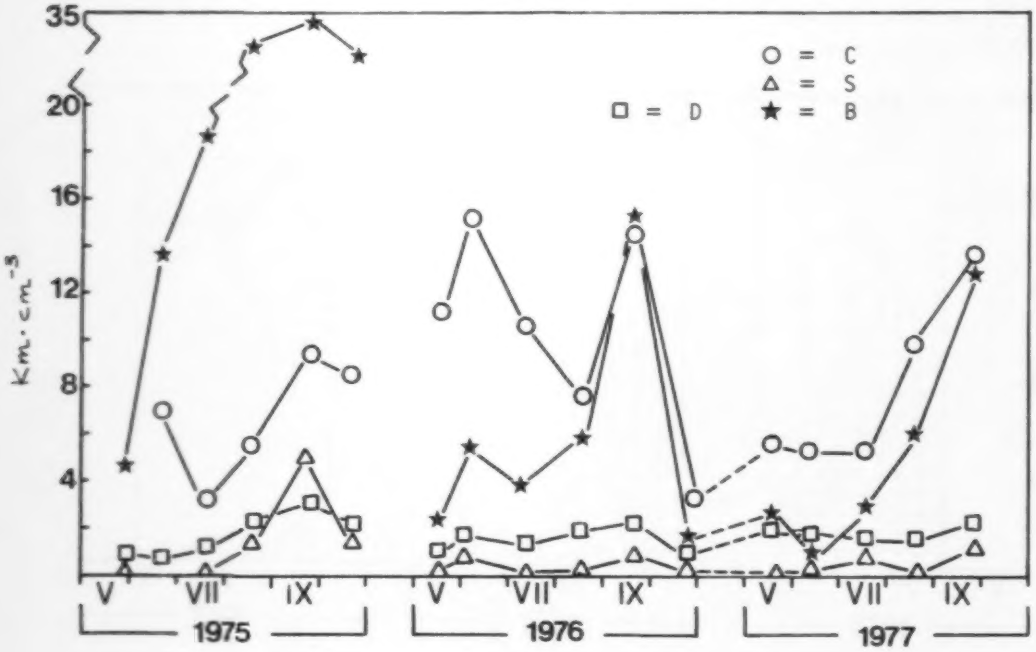
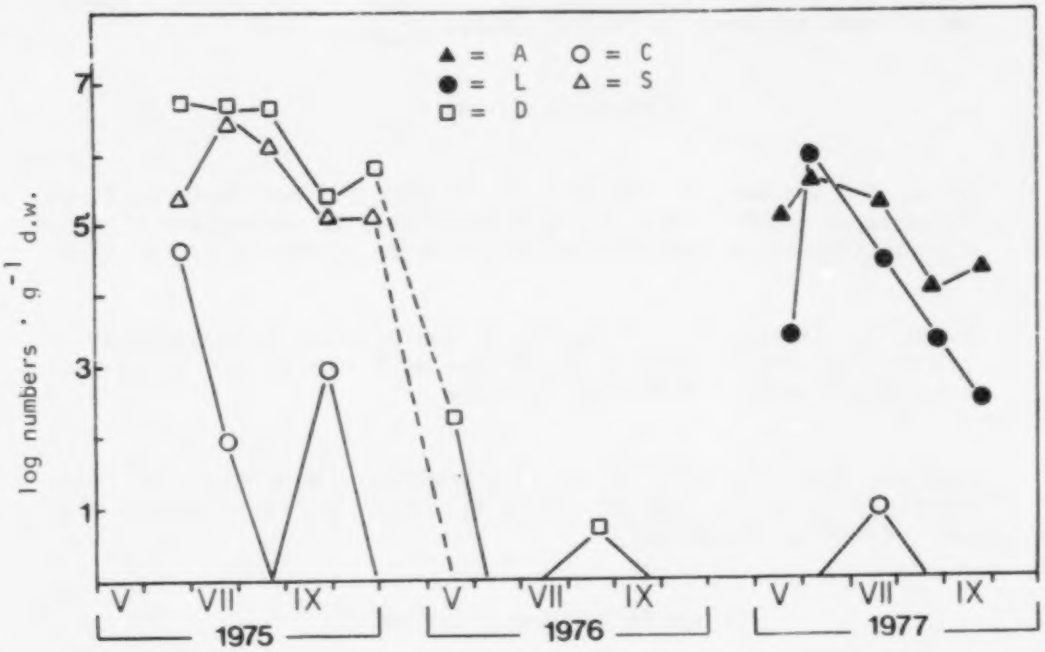


FIGURE 6. Total numbers of fecal coliforms in different materials tested. Symbols as in Figure 1. (The survey of A and L was started in 1977).



The Mesostigmata showed good ability to differentiate between the different substrates: the initial communities in the three kinds of sludge were almost totally different, and even the oldest material tested shared no common dominants with the adjacent arable soil. The Collembola proved to be least specialized: the communities of the different fresh materials were almost identical, and those of aged mixtures showed the greatest similarity to the control community.

Succession was observed not only in the ordinary test plots, but also in the reference plot established on arable soil. After remaining untreated for the survey period, it showed increasing biological activity and animal biomass from year to year (Figures 1 and 2).

The zoological part of the investigation will soon be published in greater detail (Huhta, Ikonen & Vilkamaa, in press). The microbiological part is in preparation. A report of the whole project has already appeared in Finnish (Huhta et al., 1978).

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QUESTIONS and COMMENTS

K.H. DOMSCH: Are there any significant correlations between the plant production on those different plots and soil biological parameters tested?

V. HUHTA: We tried to find out correlations between different factors with the aid of factor analysis and canonical correlation analysis, but the result was poor because the materials tested differed from each other in many respects, several factors being highly intercorrelated.

H. EIJSACKERS: Have you any explanation for the toxicity of digested and treated sludges on Lumbricidae and Encytraeidae, perhaps from heavy metals?

V. HUHTA: We made some preliminary tests on the possible effect of heavy metal content, oxygen deficiency and the Fe_2SO_4 used for precipitation, but we could not find any single factor responsible for the toxicity.

DECOMPOSITION PROCESSES IN SEWAGE SLUDGE AND SLUDGE AMENDED SOILS

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An understanding of decomposition processes in both natural and anthropogenic systems is necessary for maximizing productivity and minimizing deleterious environmental impacts. An important category of anthropogenic systems is associated with the treatment of wastewater. These facilities are used for the maintenance of water quality and also demonstrate the importance of decomposition both within the systems themselves and by their interactions with surrounding areas, including urban and agricultural communities.

The two major outputs of a given wastewater treatment facility are the treated effluent and the residual solid, defined as sludge. The characteristics of the effluent and especially the sludge vary greatly since the sewages themselves and the treatment processes differ both among and within these facilities (Mitchell et al., 1978; Sommers, Nelson and Yost, 1976). Important variables include the concentration of various human pathogens, heavy metals, organic constituents and inorganic nutrients. Although the major objective of wastewater treatment is the removal or elimination of these components from the effluent, the efficiency of this process depends on the design of each treatment facility which may utilize some combination of primary (physical settling of solids), secondary (decreasing organic constituents by biological processes) and tertiary (removing dissolved inorganic and organic substances) treatment (Eckenfelder and O'Connor, 1961). As treatment facilities have become more effective in this removal process, there has been a concomitant increase in the residual sludge which now amounts annually to about six to seven million dry metric tons in the United States (Harrington, 1978). The decomposition and resultant stabilization of this material are major factors which affect its management.

During secondary treatment, both activated sludge and trickling filters are used to stabilize and reduce the organic constituents of sewage. The actual function of these systems has been detailed elsewhere (Curds and Hawkes, 1975; Hawkes, 1963; Mitchell, 1978). In addition, the sludge, which is produced from this secondary as well as from primary and tertiary treatment, needs further processing which may include dewatering, aerobic and anaerobic digestion and disinfection. Ultimately this sludge must be managed by either disposal or further utilization. If the sludge is incinerated or dumped in the ocean, air or water pollution may occur and thus the latter disposal practice is being discontinued (Bastian, 1977).

In contrast, the deposition of this sludge on land has a variety of potential benefits including its use as a soil conditioner and fertilizer due to its organic constituents and elevated levels of inorganic nutrients including nitrogen and phosphorus. However, as mentioned previously, sludges may contain heavy metals, such as cadmium, and human pathogens which can endanger public health if they contaminate water supplies or enter the food chain (CAST, 1976; Loehr, 1977; Love, Tompkins and Galke, 1975). To maximize the utilization of sludge as a soil amendment, its decomposition processes must be delineated since they partly determine organic matter stabilization, heavy metal availability, pathogen inactivation, mineralization and even odor production. Some of the major factors which will affect the decomposition and stabilization of sludge are availability of an organic energy source, concentration of electron acceptors, moisture, temperature, inorganic nutrients, pollutants, and various biotic components. The importance of each of these factors will be discussed with regard to wastewater treatment, in general, but emphasizing decomposition of sludge and sludge amended soils.

Organic energy source availability

Wastewater solids have a high proportion of labile organic constituents which are removed in varying amounts during the treatment process. If the resultant sludge is digested anaerobically, the organic matter of the raw sludge, which ranges from 60 to 80%, is reduced to between 40 and 60% (Bolton and Klein, 1971; Eckenfelder and O'Connor, 1961; Hawkes, 1963). The production of methane by anaerobic metabolism depends on the availability of labile organic fractions such as acetate, the amount of which decreases as stabilization progresses (Mah et al., 1977). The methane produced by this process may be subsequently used as a fuel.

For aerobically digested sludges, the organic matter reduction is less and after digestion it may still constitute 62-75% of the solid residuals. The major portion of this organic matter is probably derived from microbial products (Daigger and Grady, 1977).

Another mode, which has been recently employed for furthering sludge stabilization, is composting in which the organic matter of raw sludge can be reduced about one-third under thermic and aerobic conditions (Epstein and Willson, 1975). As in all composting processes the rate of decomposition decreases rapidly as the organic matter stabilizes and humification occurs (Gray and Biddlestone, 1974).

If drying beds are used for sludge dewatering, the decomposition and humification continues within these systems. Regardless of whether the sludge is derived from anaerobic or aerobic digestion, both anaerobic and aerobic decomposition occur. Anaerobic decomposition, as indexed by methane production, predominated in the early drying phase of an activated sludge due to abundant, labile organic fractions and low oxygen. With a residence time of two weeks in these drying beds, an additional 2% reduction of the organic matter occurred during the summer at temperatures ranging from 11 to 28°C (Mitchell, Hornor and Abrams, in review).

When sludge is applied to soil the decomposition rate is also dependent upon the degree of stabilization. For example, an aerobically digested sludge lost 48% organic matter in contrast to three anaerobically digested sludges, which lost from 28 to 36% organic matter over

168 days when added to a mineral soil in a glasshouse (Mitchell et al., 1978). In microcosms and a sludge amended agricultural soil, organic matter losses of anaerobically digested sludges were 20% over 5 months (Miller, 1974) and 60% over 7 years (Hinesly et al., 1977), respectively.

Since sludge decomposition and stabilization are biologically mediated, the rate of these processes is an index of the activity of various organisms. The importance of these organisms in aerobic and anaerobic digestors has been reviewed previously (Curds and Hawkes, 1975; Mitchell, 1978). With increasing sludge stabilization there is a parallel decrease in total viable bacteria (Miller, 1974; Mitchell et al., 1978). Similarly, in sludge drying beds and sludge amended soils there is a faunal succession which is probably due to changes in food resources as well as in the physical and chemical environment. Major endemic faunal components associated with this succession include nematodes, enchytraeids and arthropods (Huhta, Ikonen and Vilkamaa, 1977; Mitchell et al., 1978, in review). Furthermore, the addition of oligochaetes, such as Eisenia foetida (Sav.), into sewage sludge will hasten sludge decomposition and their activity depends on both the age and type of sludge (Mitchell et al., 1977, 1978, in review; Mitchell, 1979).

Electron acceptor availability

There is a general trend during sludge stabilization from an excess of electron donors to an excess of electron acceptors. One of the major objectives in the activated sludge process and aerobic digestion is the maximization of the concentration of oxygen which serves as the terminal electron acceptor in aerobic respiration (Eckenfelder and O'Connor, 1961). In contrast, anaerobic digestion uses the products of fermentation, organic acids and carbon dioxide, as electron acceptors and converts them into methane and carbon dioxide (Crowther and Harkness, 1975). Therefore, the rate of methanogenesis is limited by the availability of precursors such as acetate (Mah et al., 1977).

Within sludge drying beds the availability of electron acceptors is a major factor in determining the rate of decomposition and whether aerobic or anaerobic decomposition will predominate. The rate of oxygen diffusion into sludge is highly dependent upon its moisture content as will be discussed below. It has also been shown that the addition of an alternate electron acceptor such as nitrate stimulates carbon dioxide evolution (Mitchell, Hornor and Abrams, 1980). Similarly, for composted sludge, it is generally necessary to use forced aeration to maintain a surplus of oxygen necessary for this aerobic process (Epstein and Willson, 1975).

When sludge is added to soil, it serves as a rich source of electron donors and thus may deplete oxygen and alternate electron acceptors and cause a depression of Eh and an increase in anaerobic microbial metabolites. For example, Taylor et al. (1978) found that raw sludge produced a much larger proportion of methane in the soil atmosphere than anaerobically digested sludge which would have less electron donors due to its increased stabilization. A general consequence of a depressed Eh and anaerobic conditions is the reduction of decomposition due to the lower metabolic efficiency of anaerobiosis. In addition, some of the reduced compounds may be toxic to microflora, invertebrates and higher plants and there may be a depression of carbon flux and mineralization, although certain nutrients such as phosphate may become more available (Buckman and Brady, 1969; Patrick and Delaune, 1977; Skinner, 1975). Among these reduced compounds various malodorous sulfur gases may also be produced which may restrict the application of sludge to land (Hornor, Waugh and Mitchell,this volume). In addition, the Eh will affect the availability of certain heavy metals such as cadmium (Bingham et al., 1976). It should be emphasized that the consequences associated with anaerobic microbial metabolism are not exhibited if the sludge is stabilized and proper application rates and soil conditions are maintained.

Oxygen availability will also affect the functional role of the faunal components. Nematodes, which are abundant in sludge drying beds, can survive anoxic conditions and be active at a pO_2 of 7000 dyne cm^{-2} (Abrams and Mitchell, 1978). In contrast earthworm respiration is depressed at a pO_2 of 53200 dyne cm^{-2} (Johnson, 1942). This effect was shown indirectly in a sludge drying bed where the presence of earthworms did not affect the rate of decomposition until aerobic catabolism predominated. In addition, a depression of Eh was associated with high mortality of earthworms which had been previously introduced into the sewage sludge (Mitchell et al., in review). In general, the role of various faunal components during sludge decomposition may be linked to their oxygen needs and Eh tolerance.

Moisture

During the treatment of wastewater itself, the amount of water present does not affect the decomposition process except as a determinate of the concentration of the various inorganic and organic constituents. However, in drying beds the moisture content has major importance. Because of the low solubility of oxygen in water, a sludge or a sludge amended soil with a high moisture content and elevated metabolic rate will be rapidly depleted of oxygen, the results of which were discussed previously with regard to electron acceptors.

With increased drying, oxygen availability increases, but there is a concomitant decrease in metabolic activity. Within certain thresholds, moisture content is directly proportional to decomposition rate. Similarly, as has also been documented for soils, when sludge has been rewetted, the metabolic activity is enhanced (Mitchell, 1979; Mitchell et al., in review). The importance of moisture in affecting the decomposition of sludge amended soils has been shown indirectly in a glasshouse study in which organic matter loss was greater, due to a higher moisture regime, than under natural field conditions (Hinesly et al., 1977; Mitchell et al., 1978).

The general importance of moisture for maintaining the activity of both the microflora and the fauna has been well documented for soils and it can be assumed that similar relationships would be found in sludge amended soils.

Temperature

In all decomposition processes, the effect of temperature is marked. Generally, the rate of metabolism increases with temperature within upper and lower limits which are dependent upon the constituent organisms' temperature tolerances. Within anaerobic sludge digesters 30 to 35°C is considered as the optimal range for both organic matter stabilization and methane production (Imhoff, Müller and Thistlethwayte, 1971). Temperatures of activated sludge and trickling filters are close to ambient although they may be somewhat lower in summer and higher in winter and their activity is thus closely coupled with ambient conditions. Seasonal changes in their characteristics may be partly due to these temperature fluctuations (Curds and Hawkes, 1975). In composted sludge, the temperature ranges from ambient to 80°C (Epstein and Willson, 1975).

Oxygen consumption of activated sludge taken from a drying bed exhibited an exponential relationship to temperature and a Q_{10} of 2.94 over a 5 to 30°C range. This value is within the range found for soils and aquatic sediments (Mitchell, 1979). Temperature not only directly affects microbial and faunal metabolism, but also affects population growth and interspecific interactions between the fauna and their microbial food resources (Abrams and Mitchell, this volume; Mitchell, 1979).

Although the effect of temperature on decomposition in sludge amended soils has not been studied in detail, it is widely recognized that low temperatures, especially below freezing, may limit the application of sludge in winter. Furthermore, the general effect of temperature on decomposition of sludge amended soils has been demonstrated by Miller (1974) using microcosms in which the temperature regime was directly related to decomposition rate.

Other nutrients and pollutants

Because there is a high concentration of inorganic nutrients, such as nitrogen and phosphorus, these constituents do not generally limit sludge decomposition and their presence is one of the major beneficial attributes of sludge as a soil amendment. Moreover, the mineralization rates of these nutrients will affect their availability to higher plants and determine in part the potential for ground water contamination (Koterba, Hornbeck and Pierce, 1979; Riekerk, 1978). However, both organic (e.g., phenols) and inorganic (e.g., heavy metals) constituents, depending on their concentration, may interfere with sludge decomposition and stabilization by their deleterious impact on the biota (Hayes and Theis, 1978; CAST, 1976; Imhoff et al., 1971). Such pollutants, along with pathogens, if present in sludge, may limit its utilization as a soil amendment because of potential toxic effects to both plants and animals, including man (Burge and Marsh, 1978; CAST, 1976; Harrington, 1978; Williams, Shenk and Baker, 1978).

Biota

The overall role of the microflora and invertebrate fauna in wastewater treatment is well documented (Curds and Hawkes, 1975; Hawkes, 1963) and recent studies have established basic information on their roles in sludge and sludge amended soils (Huhta et al., 1977; McIlveen and Cole, 1977; Mitchell, 1978, 1979; Mitchell et al., 1978, 1980, in review; Varanka, Zablocki and Hinesly, 1976). The importance of the biota in wastewater and sludge has been alluded to in previous sections.

The biota should be considered as a series of functional units which maximize nutrient and carbon flux. An excellent example of the interactions between these units is exhibited by the synergistic relationships between protozoa and their bacterial food sources in activated sludge where protozoa feeding stimulates the metabolic activity of the bacterial populations. The importance of similar interactions in sludge drying beds and sludge amended soils has been demonstrated for endemic nematodes and bacteria (Mitchell et al., 1980; Abrams and Mitchell, this volume) as well as introduced macroinvertebrates such as Eisenia foetida (Brown, Swift and Mitchell, 1978; Mitchell, 1978, 1979; Mitchell et al., 1978, 1980, in review). The importance of these interspecific interactions has also been shown by the introduction of an ectomycorrhizal fungus into sludge amended soil which resulted in accelerated tree growth (Berry and Marx, 1976).

Decomposition and maximizing sludge utilization

Both wastewater treatment and sludge management rely on maximizing beneficial functional relationships among the biota and their chemical and physical environment. It must be clearly recognized that these relationships are major factors in determining the efficiency of the treatment process and the subsequent utilization of sludge as a soil amendment. By minimizing those components such as heavy metals and undesirable processes such as the production of toxic compounds, the utilization of wastewater treatment and sludge management as a mechanism for soil reclamation and nutrient conservation may be fully realized.

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QUESTIONS and COMMENTS

S.E-D.A. FAIZY: How do you explain the positively linear relationship between O_2 consumption and moisture content in sludge? I believe that the increase in moisture (100 to 300%) might eventually lead to anaerobic conditions.

M.J. MITCHELL: Sludge has much higher moisture holding capacity than mineral soils. We have found that aerobic catabolism may predominate even when sludge is 300% moisture on a dry weight basis. Under conditions of high oxygen demand and low oxygen diffusion anaerobic conditions are produced.

SOIL MICROFAUNA OF OPEN DRAINS IN MID-DELTA EGYPT

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INTRODUCTION

In Egypt during the last ten years, a project was established to replace the normal open drainage system to tiles, in the whole valley. To execute this project, machinery had to deepen the ordinarily used drains and dredge the accumulated residues from the bottom of the drains, placing it on one or both sides of the ditches making a huge mound of wet soil. This process had been done previously, but on a limited scale during a specific period of winter time.

This soil-like residue is used in brick factories, or for filling in around house foundations. It is also used on a large scale as an organic fertilizer following its use as an animal bedding material.

Organic fertilizers usually do not contain poisons in toxic concentrations. Gases and heat released during their decomposition may be translated into behavioral responses among soil fauna. In addition, these organic fertilizers provide additional habitat space and food which supports micro- and mesofaunal organisms. High percentages of the total soluble salts associated with them may be harmful to plants.

Many investigators discussed the relation between fertilizer and soil, Allison (1966), Foster (1968), Behan (1972) and Behrend (1973). Others reviewed forest fertilization or the role of soil organisms in organic matter decomposition (Baule et al. 1970, Bengston 1971, Weetman 1973, and Mitchell 1978.

In Egypt, Hafez (1939) who described the insect fauna of the dung. Later on El-Kifl (1957, 1958) investigated some ecological factors responsible for faunal fluctuations.

Tadros (1965, 1976, 1978) discussed the vertical and horizontal distribution of oribatids and more ecological factors responsible for fauna populations.

This paper briefly reviews the following objectives:

a) to determine the most prevalent fauna species of dredged mud from the bottom of the drains through a 12 months period.
b) to find if there is any difference in faunal distribution in the accumulated drain residues, compared to the native fauna in the same district.
c) to find if the prepared organic fertilizer is harmful to animals, when using it as bedding in their sheds, or harmful for plantations in fields.

METHODS AND MATERIALS

Location of the Study

Two villages near the Faculty of Agriculture were chosen for this experiment. They were about 8 km (5 mi) and11 km (7 mi) from the city of Kafr El-Sheikh. An ordinary open drain was running beside these two villages. Its upper margin was about 3 m; its bottom was 1 m wide, while its depth was about 2 m. From the muddy hill, established from the machinery deepening process in that drain, a 16 km (10 mi) plot was chosen. This hill was about 2 m high. At the beginning of investigation, the site was nearly all composed of wet muddy soil. From the third month onward it was drier and some weeds grew scattered on it.

This characteristic soil, is known to be heavy, black and becomes full of cracks when dry, comprising big masses of soil. The percentage of total soluble salts is also reasonable in that sort of soil.

Techniques

It was arranged to take samples at three levels (top, middle and bottom) from the previously mounded soil residues cast from deepening the drain. Samples were taken every two weeks until the third month, then monthly until the end of investigation. At every sampling date 30 cylinders were collected, 10 from each examined level representing 10 replicates from each. Some soil samples were also tested to find some essential soil properties. More samples were also taken from the prepared organic fertilizer. The sampling and extraction precedures were just the same described by Tadros et al. (1965).

RESULTS AND DISCUSSION

Extracted Fauna

The extracted fauna was found to fall under two categories, Insecta and Acarina. The first group represented individuals from the orders, Collembola, Thysanura, Hymenoptera, Homoptera and Coleoptera, but owing to the fact that springtails comprised the majority of insects they were considered as separate sub-groups. Acarina comprised moss mites and soft bodied mites.

Total Fauna Encountered

At the beginning of experiment, no fauna existed in mud, but from 2 wks until 12 mos the extracted fauna increased (Figure 1).

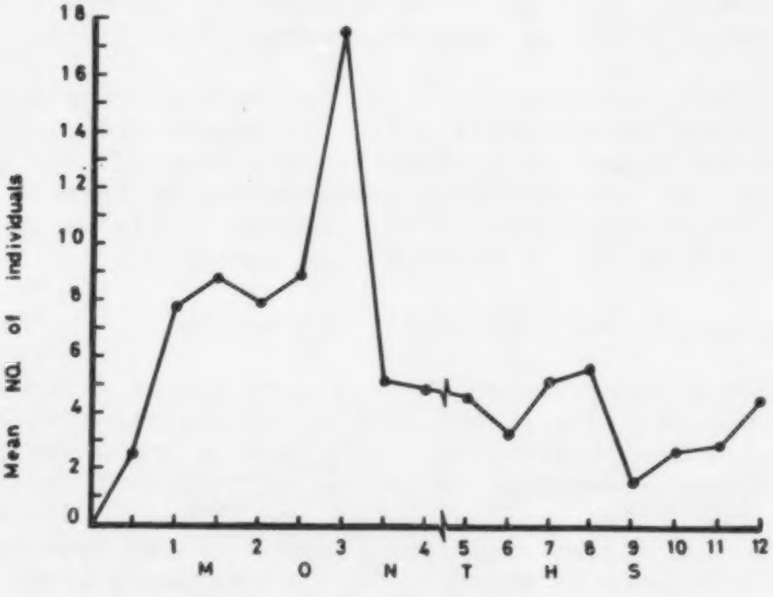

Fig.(1): Means of total fauna

It is clear that a peak occurred in the third month, with two other lesser peaks occurring after 1½ and 8 mo. These results may be due to high water content and to anaerobic circumstances in the first samples, but when the soil began to dry, organisms began to creep into it. The last peak occurring in the eighth month may be due to the scattered growing weeds at that time that gave a suitable atmosphere in which some fauna could flourish. On the other hand, the low percentage of other faunal forms during that period may be due to the low relative humidity in soil due to its dryness after that long period.

Vertical Distribution of Fauna

It was found that most of the fauna (40.9%) were in the lower level while in the middle, 31.8% of the fauna, and in the upper level, the minority of 27.3%. These results may be due to the drying by the sun and wind evaporation of water occurring more rapidly in upper regions. Also, individuals immigrate to lower regions in demand for moisture.

Faunal Groups

Springtails were found in enormous numbers in the soil. They are the base of soil animal food chain (William 1942). They can occur in all types of soil and under various vegetative cover. This group is abundant in all moist and fairly moist soils to unknown depths (Jacot 1940).

In this investigation, the springtails comprised (25.42%) of the whole fauna, while all other insect orders (32.20%). Acarina was a prevalent order in this type of soil (42.37%). Comparing the percentage of collembolans to insects, the former comprised 44.12% of the insects. This result supports the prior findings of Williams and Jacot.

Faunal Groups, Vertical Levels and Months

It was clear (Table 1) that only slight differences occurred in the 3 vertical levels tested. Insecta and Acarina tended to flourish in the middle and lower regions of soil cast residue mound during all times of the experiment (Table 2). These results may be attributed to the moisture in these two regions. It was clear from the same table that springtails were affected by both microclimatic and soil factors. This result appeared in the fluctuation of its numbers over time and in the different vertical strata.

Table 1: PERCENTAGES OF THREE MAIN FAUNA GROUPS AT 3 VERTICAL LEVELS EXTRACTED FROM MUD DREDGED FROM A DRAIN

GROUPS	UPPER	MIDDLE	LOWER	MEAN
COLLEMBOLA	25.92	24.87	25.92	25.57
INSECTA	29.62	36.51	27.16	31.09
ACARINA	45.06	39.15	46.91	43.70

The author attributes this result to the sensitivity of this group to many ecological factors.

Prepared Organic Fertilizer

Data in (Tables 3 & 4) indicates that total soluble salts (TSS) soil residues from the drain was 3.75 mm hos/cm, or rather, nearly a salty soil. It is also known, that Kafre El-Sheikh soils are somewhat alkaline, so a decrease of TSS occurred when preparing the organic manure, because of the acidity of urine and faeces of animals when using it for bedding. The percentage of both Collembola and Insecta was low in this manure when compared with that from cast drain soil; this result indicates that such acidity is not preferred by Insecta. On the other hand, Acarina flourished in manure and nearly doubled giving an impression that that environment was preferable to them.

Considering the numbers of microflora obtained (Table 4), it was obvious that Bacteria, Fungi and Actinomycete counts increased in the cast drain residues when compared with ordinary cultivated soil. This is due to the change in soil acidity, but this increase was only for a short time for a decrease was observed when preparing the organic fertilizer. The high percentage of organic matter comprising the manure may be also considered. The increase of microflora was followed by an increase of microfauna that depends upon microflora. This result was obvious from the table, for fauna became nearly five times greater when compared with that occurring in cast drain soil.

It, therefore, is not suitable to use this prepared organic matter as an organic fertilizer, for it appeared

LEVEL	GROUP	1 week	2 weeks	PERIOD IN MONTHS																
				1	1½	2	2½	3	3½	4	5	6	7	8	9	10	11	12	Tot.	Mean
UPPER	Collembola	o	0.3	0.1	0.5	1.6	1.3	0.2	0.1	0.4	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.3	6.7	0.4
	Insecta	o	0.4	0.1	0.8	0.1	0.0	0.3	0.6	0.3	0.5	0.7	1.1	1.4	0.4	0.3	0.3	0.0	7.6	0.5
	Acarina	o	0.2	1.0	1.4	1.0	3.6	0.1	0.1	1.1	1.2	1.2	0.2	0.1	0.1	0.0	0.2	0.1	11.6	0.7
	Tot. Fauna	o	0.9	1.5	2.7	2.7	4.9	0.6	0.8	1.8	2.4	3.1	1.3	1.5	0.5	0.3	0.5	0.4	25.9	1.6
MIDDLE	Collembola	o	0.4	2.6	0.5	1.2	0.0	1.2	0.0	0.0	0.7	0.2	0.5	0.0	0.0	0.0	0.0	0.1	7.4	0.5
	Insecta	o	0.1	0.5	0.4	0.2	0.2	0.0	0.4	0.8	0.0	0.7	0.6	2.7	1.0	0.6	0.7	1.1	11.0	0.7
	Acarina	o	0.4	2.2	1.9	0.3	2.3	0.8	0.8	0.7	1.1	0.0	0.4	0.2	0.0	0.1	0.2	0.4	11.8	0.7
	Tot. Fauna	o	0.9	5.3	3.8	1.7	2.5	2.0	1.2	1.5	1.8	0.9	1.5	2.9	1.0	0.7	0.9	1.6	30.2	1.9
LOWER	Collembola	o	0.0	0.0	0.5	1.7	0.3	4.9	1.4	0.7	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	10.1	0.6
	Insecta	o	0.0	0.5	0.0	0.5	0.5	1.8	0.9	0.4	0.2	0.2	1.2	1.2	0.1	1.3	0.9	0.9	10.6	0.7
	Acarina	o	0.7	0.4	1.8	1.3	0.7	8.3	0.9	0.5	0.2	0.1	0.8	0.1	0.0	0.4	0.6	1.4	18.2	1.1
	Tot. Fauna	o	0.7	0.9	2.3	3.5	1.5	15.0	3.2	1.6	0.4	0.3	2.4	1.3	0.1	1.7	1.5	2.5	38.9	2.4
Tot. Fauna in 3 levels		o	2.5	7.7	8.8	7.9	8.9	17.6	5.2	4.9	4.6	4.3	5.2	5.7	1.6	2.7	2.9	4.5	95.0	5.9

Table 2: EXTRACTED FAUNAL GROUPS FROM THREE SOIL STRATA OVER AN ANNUAL PERIOD (no. in means)

Table 3: MEANS AND PERCENTAGES OF 3 MAIN EXTRACTED FAUNA GROUPS IN PREPARED ORGANIC FERTILIZER AND CAST DRAIN SOIL

GROUPS	ORGANIC FERTILIZER		CAST DRAIN SOIL	
	Mean/sample	%	Mean sample/	%
COLLEMBOLA	0.23	22.80	0.50	25.51
INSECTA	2.30	22.77	0.63	32.14
ACARINA	7.57	74.95	0.83	42.35
TOTAL	10.10	-- --	1.96	-- --

Table 4: MICROFLORA AND MICROFAUNA IN THREE APPLICATIONS WITH TWO SOIL PROPERTIES

			means · gm^{-1} soil				
	pH	Total Soluble Salts	Bacteria	Fungi	Actino-mycetes	Total Microfauna Mean	%
CONTROL	7.56	1.11	2×10^6	1.17×10^5	2.5×10^5	3.66	23.28
CAST DRAIN SOIL RESIDUES	6.20	3.75	12×10^6	4.5×10^4	3.75×10^4	1.96	12.47
ORGANIC FERTILIZER	6.65	2.60	6×10^6	2.3×10^5	2.5×10^5	10.10	64.25

that it contains a high percentage of TSS that may be harmful to both soil or plants, especially if it is used more than once in somewhat alkaline soils. Its injury may also affect sensitive animals for the same reason discussed.

SUMMARY

An evaluation of fauna existing during a year in dredged and mounded muds from an open drain was researched. As this soil is transferred to organic fertilizer when using it as an animal bedding in their sheds, fauna was also estimated in it, plus accompanying soil cultivated with ordinary crops. Soil properties that were suggested to affect fauna, was also estimated.

The results indicated that no fauna was present in the mud residues until the third month. Extracted fauna was found to fall under two orders: Insecta and Acarina. Springtails comprised a reasonable fraction of insects. It was suggested that this type of soil is not preferable in use as an organic manure especially in the somewhat alkaline soils with high water table. On the other hand, this soil can be used in brick factories or filling up house foundations.

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LEAD AND CADMIUM CONTENT IN EARTHWORMS (LUMBRICIDAE) FROM SEWAGE SLUDGE AMENDED ARABLE SOIL

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ABSTRACT

From 1976 to 1978 a research programme has been carried out in order to investigate the uptake of the metals Lead and Cadmium in earthworms from sewage sludge amended arable soil. Two types of sewage sludge were used in the experiment. One with a low metal content and one with a high metal content, derived from an industrial area of Northern Copenhagen. Additionally was studied *Lumbricus terrestris L.,1758*,from the garden of The Royal Veterinary and Agricultural University in central Copenhagen with heavy Lead pollution from automobile emission. Metal content was measured in whole earthworm tissue, waste bodies from the posteriormost region, gut walls, soil, sewage sludge and earthworm casts. In general Lead is not concentrated in earthworm tissue, whereas Cadmium is strongly concentrated. *Allolobophora longa Ude,1886*, seems to exploit the sewage sludge-N supply very extensively. Frequencies of the individual species from the sewage sludge treated plots were compared to plots receiving slurry and farmyard manure.

INTRODUCTION

As a result of the increasing interest paid to the recycling of waste water and sewage sludge in agricultural practice, a great effort has been done to study the uptake of heavy metals in crops for human food. In this connection there is also a need to study the general impact of these metals on the soil life, because good soil conditions and plant growth as revealed by several investigations are intimately associated with soil life.

Dindal, Schwert and Norton, 1975, found that waste water irrigation caused a shift in soil fauna biomass towards earthworms and a general decrease in species diversity. Earthworms are preyed upon by a great number of animals and may become a potential source of pollution for these in an increasingly polluted environment. Getz, Best and Prather, 1977, found highly increased Lead levels in starling kidney and liver from urban environments.

In the present study is reported on uptake of Lead and Cadmium in earthworms from sewage sludge amended soil and the influence on species composition. The uptake of these metals was also studied in *L. terrestris* from the garden of The Royal Veterinary and Agricultural University (RVAU) in central Copenhagen, adjacent to a main street with intense automobile traffic. The investigations were supported by the Danish Research Council, SJVF.

METHODS and MATERIALS

Sampling and treatment

Earthworms for metal analysis were sampled in sewage sludge experiments performed at Askov Research Station, Southern Jutland, in June and October 1977. Two types of sewage sludge were used, 1) one with low metal content and 2)one with a high metal content, indicated in Tables 1 to 3 by (L) and (H) respectively. Material for metal analysis was obtained by digging. Material for species and biomass determination was extracted by the formalin technique using 0.5 m^2 sampling quadrat. Eight sampling units were taken per treatment, which also include a 0-treatment. The sewage sludge was given in amounts equivalent to 30 tons sand free dry matter/ha, and contains approximately 1000 kg N/ha. The following species were obtained: *A. longa*, *A. caliginosa Savigny, 1826*, *A. rosea Savigny, 1826*, *A. chlorotica Savigny, 1826*, and *Lumbricus terrestris*.

Material of *L. terrestris* was sampled by the formalin extraction technique in the RVAU-garden at stations 10, 20, 30, 40 and 50 metres from the side of a main street with intense automobile traffic.

Preparation of samples and extraction

From the sewage sludge experiment were taken subsamples of earthworms containing from 10 to 35, depending on size. Lead, Cadmium and Calcium were extracted from worms, sewage sludge, soil and casts of *A. longa* by wet digestion in nitric-perchloric acid with subsequent analysis by atomic absorption spectrophotometry (Andersen, 1979 in press). From *A. longa* waste bodies located in the coelomic sacs of the posteriormost region were isolated by dissection. Likewise gut wall material was isolated from behind the gizzard in *A. longa* and *A. rosea*. Metals from waste bodies and gut material were extracted by wet digestion in 1 ml nitric-perchloric acid (4:1) in test tubes placed in an aluminium block heated on a hot plate, 3 hours at 80°C, 2 hours at 110°C and 1 to 2 hours at 180°C for evaporating most of the extracting solution. After cooling metals were quantitatively transferred to test tubes with glass stoppers in 3 x 1 ml 2N HNO_3 diluted (1:20) in double deionized water. Then were added 1 ml Na-citrate buffer and 1 ml 1% DDDC (Diethylammonium.N.N. diethyldithiocarbaminate) in xylene, an organic compexbinder. The solution was shaken for not less than 2 minutes, with subsequent analysis by AAS.

From the RVAU-garden material of worms and soil were taken six subsamples per station for metal analysis. Each subsample of worms contained from 3 to 5 mature individuals. Soil pH was determined in $CaCl_2$.

RESULTS

Metal content of worms and soil from the sewage sludge experiment is given in Table 1. In Table 2 is given metal content in *A. lon-*

ga casts, sewage sludge and the top 5 cm soil (soil/sewage sludge) mixture from the experimental field. Data in Tables 1 and 2 are combined from June 1977 and October 1977. Number of subsamples are from 2 to 7 except in *A. rosea* 0-treatment, and *A. chlorotica* where there was only material for one. Neither was there sufficient material for analysis of *A. caliginosa* and *A. chlorotica* from the 0-treatment. In Table 3 is given metal content in waste bodies and gut wall material. Whole body and gut wall material was isolated from material fixed in 4% formalin and stored for one year in 70% alcohol. Lead and Cd content in the storage liquid was neglectible, 60 ppb Lead and 9 ppb Cd. In Table 4 is given Lead, Cadmium and Calcium content in *L. terrestris* and soil, including soil pH from the RVAU-garden. In Figure 1 number and biomass of earthworms from the sewage sludge experiment are given. It is seen that *L. terrestris* is also included here, but material for metal analysis was insufficient. The reason for this is that *L. terrestris* is difficult to obtain in sufficient numbers for analysis by digging. In Figure 2 Lead is plotted against Calcium in *L. terrestris* from the RVAU-garden. It is seen that there is a weak correlation between Lead and Calcium content $r = 0.5113$, $p < 0.01$, $y = 0.0035\,x + 0.9106$. There was no correlation between Cadmium and Calcium content.

TABLE 1. Askov Research Station. Metals (ppm dr.w.) in earthworms and soil.

	A. longa		*A. rosea*		*A. chlorotica*		*A. caliginosa*		Soil	
Treatment	Pb	Cd	Pb	Cd	Pb	Cd	Pb	Cd	Pb	Cd
0	3.8	11.8	3.2	26.9	-	-	-	-	15.3	0.29
SLUDGE (L)	4.6	5.7	4.7	10.9	4.6	10.9	6.4	6.9	28.2	0.65
SLUDGE (H)	5.9	9.2	5.5	19.6*	5.8	16.2	9.2	10.9	38.9	0.99

*Significantly higher than sludge (L).

TABLE 2. Askov Research Station. Metals (ppm dr.w.) in casts of *A. longa*, sewage sludge and soil.

	SLUDGE		CASTS		SOIL	
Treatment	Pb	Cd	Pb	Cd	Pb	Cd
0	-	-	13.2	0.14	15.3	0.29
SLUDGE (L)	396	14.6	45.0	0.53	28.2	0.65
SLUDGE (H)	2425	25.0	105.0	1.60	40.0	0.99

TABLE 3. Askov Research Station. Metals (ppm dr.w.) in *A. longa* waste bodies and gut wall, and *A. rosea* gut wall.

	A. longa WASTE BODIES		*A. longa* GUT WALL		*A. rosea* GUT WALL	
	Pb	Cd	Pb	Cd	Pb	Cd
Treatment						
0	60.0	15.4	31.4	16.1	12.0	16.1
SLUDGE (H)	89.2	12.9	31.6	15.0	23.7	15.0

TABLE 4. RVAU-garden. Soil pH. Metals (ppm dr.w.) in *L. terrestris* and soil. 10 to 50 metres from the roadside.

	SOIL				*L. terrestris*		
	pH	Pb	Cd	Ca	Pb	Cd	Ca
Metres							
10	6.93	203	1.04	25300	23.7	21.0	5000
20	7.08	179	0.76	23000	13.3	30.8	3000
30	7.21	148	0.72	24000	18.9	32.5	4700
40	7.40	66	0.29	24000	7.2	29.1	2900
50	7.28	90	0.45	16100	8.9	12.5	4500

DISCUSSION

From Figure 1 it is seen that number and biomass per m^2 is high for the species *A. longa* and *L. terrestris*. *L. terrestris* is primarily a feeder on dead leaf material, but will to a high degree also feed on the sewage sludge. When these data are compared with plots receiving farmyard manure with approximately the same nitrogen content (1000 kg N/ha) (Andersen in press) it is also seen that the number of *L. terrestris* is slightly lower, but biomass higher and that the proportion of adult biomass is very high compared to the condition in farmyard manure. In slurry both number and biomass of *L. terrestris* are very low. It may therefore be concluded that sewage sludge suppresses reproduction in this species. In *A. longa* the proportion of adult biomass is much smaller. Apparently this species is not a surface feeder as *L. terrestris*, but nevertheless appears to have a preference for particulate organic matter, and becomes dominating in sewage sludge. In farmyard manure treated plots it is likewise seen that the number of biomass of *A. longa* is greater than in slurry treated plots, which fits well with this interpretation. From Table 2 it is also seen that casts of *A. longa* contain considerable amounts of Lead and Cadmium compared to the content of the sewage sludge treated soil. It is therefore concluded that *A. longa* actively locates and eats the sewage sludge.

Upon dissection it is seen that in the posteriormost 10 or more segments in *A. longa* the coelomic sacs were densely packed with waste material. These waste bodies on microscopic examination appear

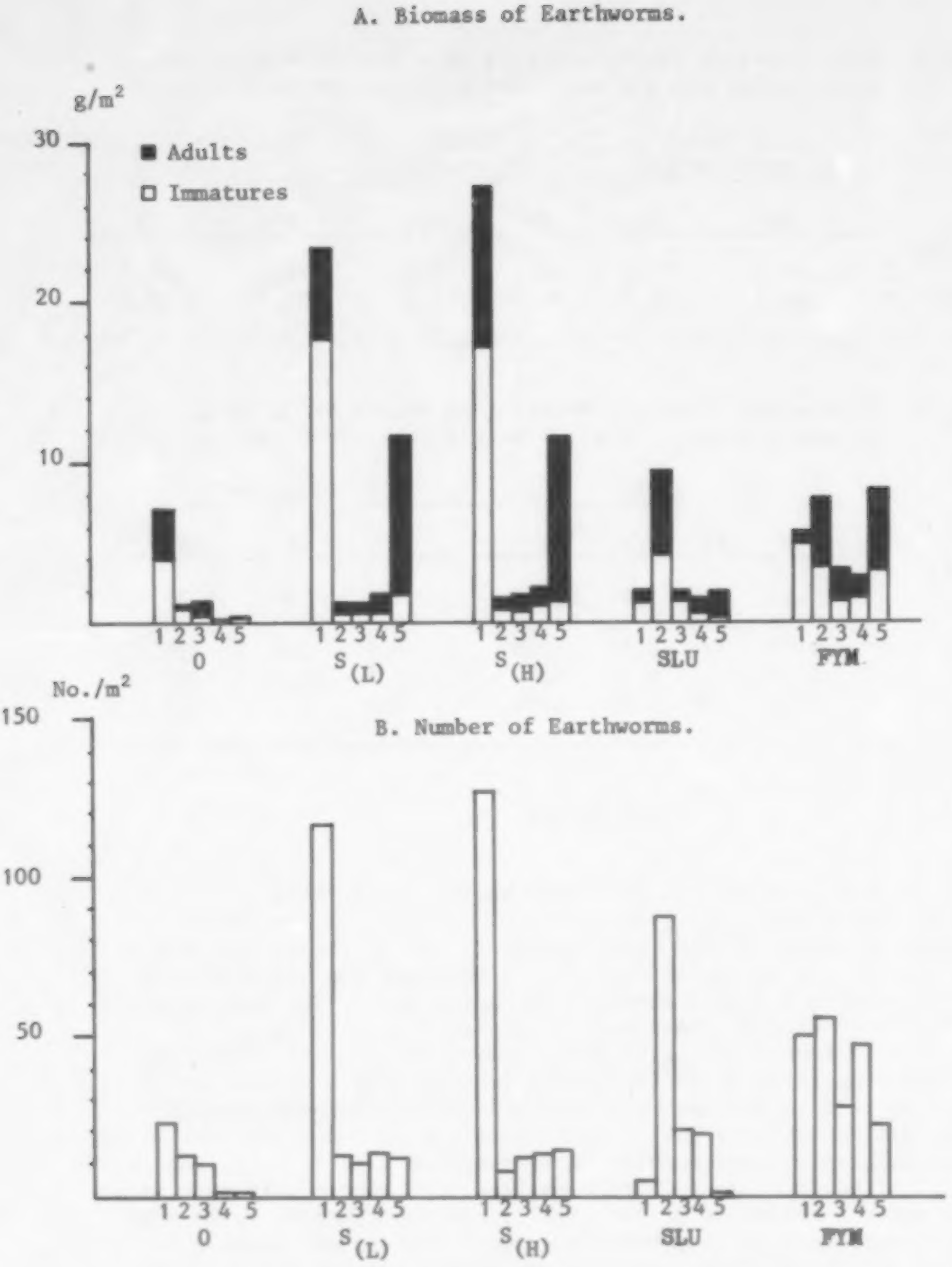
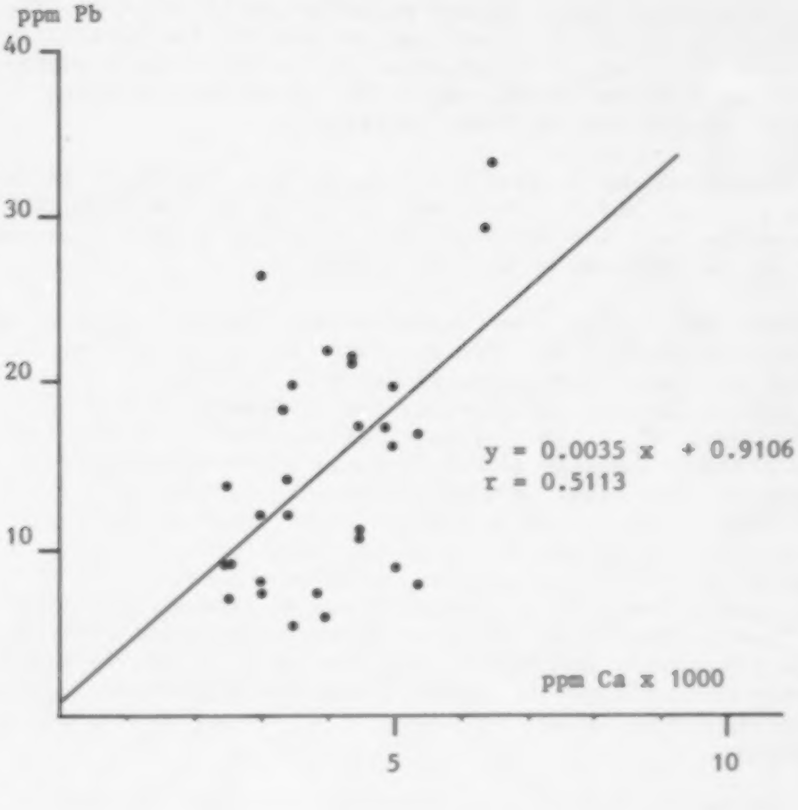


FIGURE 1. A. Biomass g/m^2 in June 1977 of the Earthworms: 1)*A. longa*, 2)*A. caliginosa*, 3)*A. rosea*, 4)*A. chlorotica*, 5)*L. terrestris* from the following treatments. 0 = zero-treatment. $S_{(L)}$ = sewage sludge with low metal content. $S_{(H)}$ = with high metal content. FYM = farmyard manure, 1000 kg N/ha. SLU = Slurry 1000 kg N/ha. The N content of sludge was approximately 1200 kg N/ha.

FIGURE 2. Regression of Ca against Pb content in the Earthworm *Lumbricus terrestris* from the garden of the Royal Veterinary and Agricultural University, Copenhagen, adjacent to a main street, sampled at distances from 10 to 50 metres from street. The correlation coefficient r = o.5113 is weakly significant $p < 0.01$ at $n = 29$.



to be surrounded by a membraneous structure and can easily be drawn out of the coelomic sacs with a needle. The waste bodies possess a very heterogeneous structure and have a Lead content which is extraordinarily high compared to the content of the worm in toto. (Table 3 and 1; 90 ppm Lead versus 6 ppm). The origin of these waste bodies is not clear, but they may represent transformed nephridia, which is now being investigated. Material of *L. terrestris* also possesses such waste bodies. In *L. terrestris* there appears to be a number of smaller packages in the last five to eight coelomic sacs as opposed to *A. longa* where two or three large waste bodies fill up the entire space of the coelomic sacs in the ten posteriormost segments. Metals, however, were not analysed in *L. terrestris* waste bodies, but as seen from the better reproduction in *A. longa* this species may be more effective in immobilizing harmful substances in this way. This phenomenon may be part of an evolutionary strategy in especially *A. longa*, being more dependent on processing large quantities of soil than *L. terrestris*, and therefore more exposed to pollution of any kind. The posterior end may be easily lost and regrown, and harmful substances accumulated in this way may be eliminated. The number of such waste bodies present may also be age-dependent. The occurrence of waste bodies in other species has not been investigated.

High concentrations of Lead and Cadmium were also found in the gut wall from *A. longa* and *A. rosea*. But the difference in Cadmium content between gut wall and whole animals inclusive waste bodies was not so great as the differences in Lead content.

A. rosea, Table 1, is seen to concentrate Cadmium from the external medium with a factor 100 from untreated soil, but only with a factor 20 from soil receiving sewage sludge with high metal content. In *A. longa* Cadmium is also concentrated mostly from untreated soil, concentration factor 40. It thus appears that Cadmium is relatively strongly immobilized in sewage sludge compared to untreated soil. This is consistent with other investigations showing that Cd^{++} is strongly adsorbed to litter and decomposed plant material (Somers, 1978) and humus (Tyler, 1972). In individuals from soil treated with sewage sludge with a high metal content, Cadmium content is higher than in individuals from soil treated with sewage sludge containing less metal. This is seen in all species. However, variation between subsamples is very great, and only in the case of *A. rosea* the difference between the two types of sewage sludge was significant. (Table 1). This great variation may be caused by uneven age distribution in the subsamples.

In *L. terrestris* from soil polluted by automobile traffic in the RVAU-garden metal content in general is highest (Table 4) close to the street. From Table 4 it is seen that soil pH is increasing from 6.93, ten metres from the street, to 7.40 at 40 metres' distance, however, with a drop to 7.28 at 50 metres' distance. Soil Ca is generally high and the low pH values closest to the street may be ascribed to acid pollution from the motor traffic.

Calcium content in *L. terrestris* was analysed, because Calcium metabolism and Lead content may be associated. Recent studies have shown that the chloragosomes of the chloragog tissues in *L. terrestris* (Prentø, 1979) may play an important role in Calcium metabolism in this species, pH regulation and ionic and osmotic regulation of the body fluids. A regression of Lead against Calcium in the RVAU material showed a weak correlation between Lead and Calcium content $r = 0.5113$, $p < 0.01$. Figure 2. Studies by Ireland (1975) have also indicated this relationship. His studies were made in highly polluted Calcium deficient soil, and at soil pH values well below 5. Therefore the correlation under nearly neutral conditions will not be so strong. In the RVAU-garden the earthworms seem to have unlimited access to Calcium, but in the worms living closest to the street some Calcium must have been used in stabilizing the internal milieu. pH of blood and coelomic fluid is supposed to be slightly alkaline, pH = 7.3 to 7.4 (Drewes and Pax, 1974). This increased Calcium turnover will then result in an elevated Lead level. The activity state of the worms may also play a role in determining content of metals. In material of *L. terrestris* from the RVAU-garden Calcium content was higher and Lead content lower during reduced activity in December 1977 compared to levels in active worms sampled in June 1978 (Andersen, 1979), but mechanisms by which earthworms maintain salt and water balance under normal conditions of partial dehydration in the soil are little studied (Oglesby, 1978).

From the foregoing discussion it is seen that the uptake pattern of heavy metals in earthworms is a complicated matter and may vary between species. Also different external factors are very important, notably soil pH and concentration of Calcium, including different food sources of the earthworms. With respect to the question of earthworms being a source of contamination for other animals it seems clear that various birds and small mammals feeding on earthworms living in sewage sludge treated soil will be subjected to ingestion of considerable amounts of Lead from the gut content and also Cadmium concentrated in the tissue of the worms. Therefore communities being associated with recycling of sewage sludge should be further studied.

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QUESTIONS and COMMENTS

N. BEYER: Would you expect that cadmium concentrations in earthworms would increase with time, as the organic matter is gradually broken down after an application of sludge?

C. ANDERSEN: Yes there is a possibility that Cd may become mobilized if the sewage treatment is interrupted.

S.G. RUNDGREN: In fact the concentration of lead is much higher in specific organs. We have made several analyses of organs showing that there is a concentration and magnification of lead in organs such as cerebral ganglion and reproductive tissues.

C. ANDERSEN: Yes we have also pursued this possibility but are unfortunately not able to present any results at this time.

K. VOSS-LAGERLUND: Do you think you can use the Cd-level in earthworms as a reliable indicator on Cd-pollution in general? Will this be an inexpensive method in the future?

C. ANDERSEN: This is a possibility but further studies are needed on the dynamics of cadmium with respect to localization in specific compartments of different species of earthworms.

VERMICOMPOSTING ON A HOUSEHOLD SCALE

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INTRODUCTION

The organic component of household garbage contributes to increased loads in solid waste disposal operations and, through garbage disposals, in wastewater treatment plants. Either form of disposal, burying in landfills or flushing it down the drain, wastes potentially valuable nutrients for plant growth. Gardeners who compost recognize the value of recycling these organic wastes. During winter months in colder areas, however, many "composters" seek other ways to dispose of their garbage because they cannot get to their compost piles through the snow. Previous work by the author (unpublished, and Appelhof, 1974) has shown that two pounds of earthworms can process a pound of garbage a day. This figure is supported by Roy Hartenstein's work with sewage sludge (Hartenstein, 1978) and Ronald Gaddie's work with larger quantities of worms on city refuse (NEWSWEEK, 1976).

This project was designed to demonstrate that household garbage can be readily composted indoors during the winter, using earthworms to process the garbage and convert it to humus. An experiment was set up to determine whether it was feasible to carry this out on a larger scale than that of a single household.

MATERIALS AND METHODS

Three wooden bins were constructed of 3/4 inch plywood: two single family bins (SFB) 30.5 x 61 x 91.5 cm (1 x 2 x 3 ft) and one multiple family bin (MFB) 30.5 x 76.5 x 245 cm (1 x 2½ x 8 ft). One-half inch holes were drilled in the bottom for aeration. Bins were placed on legs with casters for convenience.

Shredded cardboard bedding (WORM CHOW from Worm World Denver, Colorado) was soaked in water, wrung out by hand, and placed in the MFB and SFB A to a level of approximately 20 cm. Newspaper shredded by hand, soaked in hot water, and wrung out was used in SFB B to determine whether this readily available material could also be used as a bedding.

Redworms (Eisenia foetida) donated by the Southwestern Michigan Worm Growers Association were used as follows: 9 kg (20 lbs) in the MFB, and 0.9 kg (2lbs) in each SFB.

Household garbage from six low income families was buried weekly for 14 weeks; two families used the two SFB's, four to six families the MFB. pH was tested using pH paper (Hydrion Vivid 6-8 range , Microessential Laboratories). Moisture was determined empirically by squeezing a handful of bedding. A stream of water or definite sogginess at the bottom was felt to be too wet, extreme dryness on top, too dry. Burlap used to cover the bedding reduced excessive evaporation of moisture and curtailed undesirable odors. Bins were watered as needed. Participants weighed and buried the garbage, tested pH, checked moisture, and watered the bins.

A spectral analysis of the bedding for nutrient value was obtained, and a sample was taken of the completed compost. Worms were separated from the compost and bedding to be weighed on week 16. Compost and worms were distributed among the participants during week 17.

RESULTS

The amount of garbage buried per week and pH of the bedding are shown in Table I. In the MFB, a total of 78.2 kg was buried over a period of 14 weeks, averaging 5.58 kg/wk, or 1.35 kg (2.97 lb)/family/wk. Of the SFB's, one received a total of 30.8 kg, averaging 2.3 kg (5.3 lb), the other a total of

TABLE I. pH OF BEDDING AND AMOUNT OF GARBAGE BURIED PER WEEK

	MULTIPLE FAMILY BINS			SINGLE FAMILY BINS			
				SFB A		SFB B	
Week	kg garbage	# fam.	pH	kg garbage	pH	kg garbage	pH
1	3.4	5	6.9	1.3	6.6	3.5	6.6
2	5.1	5	6.6	5.6	6.6	2.2	6.0
3	8.4	5	6.6	3.9		1.5	6.9
4	7.2	5	6.3	2.0	6.4	1.7	7.4
5	6.5	5	6.4	1.5	6.9	2.3	7.6
6	8.4	4	7.4	1.6	7.0	1.4	7.2
7	5.3	4	6.8	1.8	7.4	1.5	7.4
8	7.0	4	6.9	2.1	7.6	1.5	7.6
9	5.4	3	6.8	0.8	7.0	2.2	6.8
10	4.2	4	7.4		7.2	1.4	6.4
11	7.1	4	7.0	5.6	7.1	2.7	7.6
12	3.5	3	6.8	2.6	7.2	1.4	7.4
13	3.9	3	7.2	2.0	8.0	2.1	8.0
14	2.8	4	7.2				
Total	78.2	58		30.8		25.4	
Mean	5.58/wk	1.35/fam/wk		2.37/wk		1.95/wk	

25.4 kg, averaging 1.95 kg (4.3 lb) per week. pH of the bedding ranged from 6.3 to 8.0.

Considerably less garbage (1.35 kg/fam./wk) was buried in the multiple family bin than in either of the two SFB's (2.37 and 1.95 kg/wk).

Initial and final weights of worms, total amount of garbage buried, and compost obtained appear in Table II.

TABLE II. AMOUNTS OF GARBAGE BURIED, COMPOST OBTAINED, AND WORMS USED (kg)

	MFB	SFB A	SFB B	Total
Garbage buried	78.2	30.8	25.4	134.4
Compost	76.8	16.0	23.2	116.0
Initial worms	9.0	0.9	0.9	10.8
Final worms	2.25	1.05	0.79	4.09

Total wet weight of worms and compost was 116 kg. Contributing to this weight was the original bedding (weight unknown), and 134.4 kg garbage. Whereas bins were originally set up with 10.8 kg worms, only 4.09 kg were harvested. The presence of many young worms and capsules in the bedding indicated that reproduction did take place.

Types of garbage buried were lettuce, cabbage, celery, beet greens, citrus rinds, banana peels, cereals, beans, bread, egg shells, moldy leftovers, apple and potato peels, and over 40 different kinds of kitchen garbage. Meat scraps and bones were not generally included, although on at least one occasion chicken bones were buried.

On a qualitative basis, shredded newspaper appeared to provide a satisfactory bedding, although it dried out more readily on top and was more difficult than shredded cardboard to prepare.

DISCUSSION

This work served to demonstrate to the participants and to thousands of others that earthworms can effectively convert household garbage to compost, indoors, within a four month period, and with almost no objectionable odor. Participants, all members of low income families, were able to distinguish and separate acceptable organic materials from unacceptable materials such as rubber bands, foil, plastics. They were also able to comprehend the need for and maintain the rigors of weekly trips to the Kalamazoo Nature Center to weigh the garbage, check pH, and water the bins. One motivation for their continued enthusiasm and participation was the fact that each participant would receive a share of the compost to use in her garden and/or on houseplants.

There is no question that, combined with the work of microorganisms, molds, fungi, and other decomposers, the garbage is effectively processed by earthworms. How much they can handle, or how much a given quantity of worms requires to maintain its biomass is still unknown. The great reduction in biomass in this experiment (greater than one-half) may be attributed to inadequate nutrition. The experiment was designed assuming that each family would contribute about 450 g garbage/day, or about 3 kg/wk. The results show that less than half this amount was fed to the worms. Whereas six families could have buried garbage in the MFB, only four did; since these four contributed less than half the expected amount, the worm biomass far exceeded the mass of food to eat.

The original worm population did reproduce--many capsules and young worms were seen in the bedding. The greater nutritional needs of this larger population were most likely not met, and may further explain why biomass was reduced so drastically. Other possibilities are that worms were dying from toxic conditions created in the beds from their own castings, lack of calcium in the environment, and lack of soil.

CONCLUSIONS

Household garbage from six low income families was effectively converted by 10.8 kg redworms (Eisenia foetida) to worm castings and compost over a 16 week period. The average amount of garbage buried/family/wk was 1.6 kg (3.5 lb), for a total 1f 134.4 kg (298 lb) over 14 weeks. Both shredded cardboard and newspaper served as satisfactory beddings. Wet weight of the compost produced was 116 kg. Further work needs to be done to determine optimum worms/garbage/bedding ratios.

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RECULTIVATION OF REFUSE TIPS: SOIL ECOLOGICAL STUDIES.

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Many problems arise with the recultivation of a refuse tip and its preparation for later commercial or public use. They are related to the underlying material (garbage etc.), to the new artificial topography of the dump and to the undeveloped soils of the refuse tip cover.

In order to find a basis for ecological recultivation measures on refuse tips, soil ecological studies on test sites in the vicinity of Bremen, FRG, have been undertaken (temperate climate, precipitation 728 mm/yr, average temp. 9°C). Three selected studies are presented, two as preliminary reports.

The influence of methane on the immigration to refuse tips by Lumbricids

Research site and methods

Six waste disposals, controlled tips as well as uncontrolled uncovered tips were examined with special reference to the earthworm fauna.

The formalinmethod according to Raw was used (Raw, 1960). Sample squares were 0.25 and 0.125 m^2. The biotop study was done during April and June 1978. Soil air conditions were measured with Dräger ,Gasspürgerät Mod 21/31.

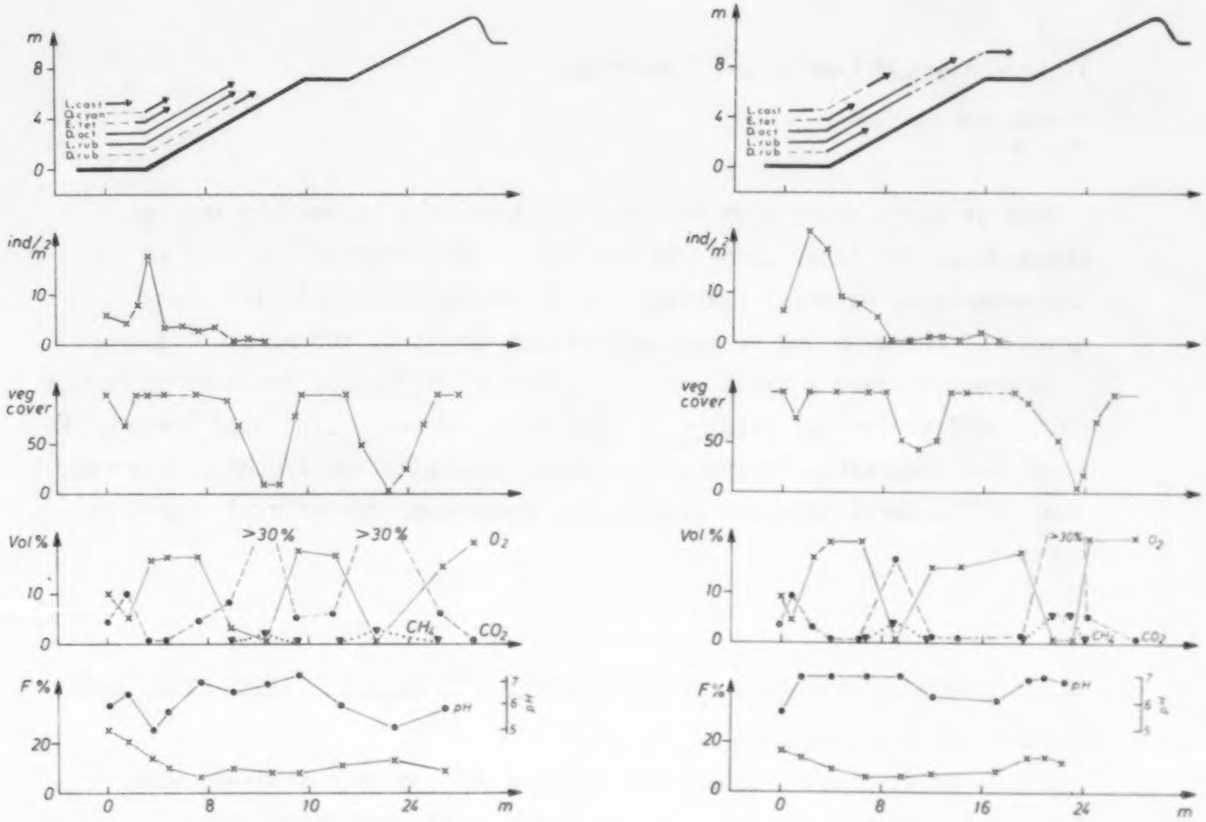
Two sites of different age (3 yrs and 5 yrs after covering) on the same refuse tip were investigated in respect to immigration mechanisms out of the surrounding habitats.

Results and discussion

Figure 1 shows the state of immigration, the abundance, the vegetation cover and the soil-air conditions. Lumbricus rubellus and Dendrobaena octaedra (south exposition) are the important colonizing species on this covered waste disposal. Horizontal - and deep burrowers are unimportant. Eisenia tetraedra was frequently found in the zone of percolating water.

The immigration speed is about 4 m/yr towards the tipplateau.

On the covered waste disposals the immigration of the soil cover by earthworms is hindered by bad soil aeration.



covered in 1975

covered in 1973

FIGURE 1: Immigration of Lumbricids on two sites of different age (3 and 5 years after covering) on the same refuse tip slope. Graphs from top to bottom: State of immigration, abundance, vegetation cover, soil-air conditions, soil-moisture (F) and soil-activity.

The study has shown, that earthworm-immigration is affected by O_2-concentrations below 15 col% and CO_2-concentrations of more than 6 vol% (15 cm depth).

Methane and carbondioxyd production from the underlying waste force out the atmospheric oxygen even of upper soil layers (Tabasaran, 1976).

Damage on the vegetation was observed when O_2-concentrations were less than 15 vol%.

The correlation analysis shows both high significance between O_2-concentration and vegetation cover as well as between O_2-concentration and abundance of earthworms. It is not known whether the immigration is hindered directly by the bad soil aeration or indirectly by the absence of plant cover.

The influence of soil cultivation and compaction on the Enchytraeid community (prel. rep.)

Introduction

The negative effects of soil compaction on terrestrial invertebrates are evident (Wilcke, 1963). In field and laboratory investigations on soil animals (Acari, Collembola, etc.) a decrease in numbers was found when compacting clay grassland soil (Aritajat et al., 1977). This report shows preliminary results of field experiments on Enchytraeidae after mixing and compacting clay grassland soil. The transported and disturbed soils of waste tip covers are characterized by destruction, drainage and compaction of the habitat the soil fauna lives in. These factors may cause difficulties in recolonization and erection of a terrestrial ecosystem of high stability.

Research site and methods

Preinvestigations were done in July and August 1978 on a clay grassland soil within an area of 8 x 24 m. For treatment this range was splitted into three equal test plots (64 m^2) on the 16.9.1978. Plot 1: remained untreated. Plot 2: soil was loosened down to 15-18 cm by rotary cultivation. Plot 3: treated like plot 2 and once compacted with an UNIMOG tractor (1.01 kp/cm^2).

Samples were taken randomly at intervals of two weeks and one, three, six and nine months after the treatment. Twelve soil cores each with 20 cm^2 surface and 15 cm depth were examined from the three test plots and divided into 5 cm layers. These 100 cm^3 samples were extracted in an apparatus functioning according to the method of O'Connor (O'Connor, 1962).

Results and discussion

Results (FIGURE 2) are means of 12 samples. The distribution pattern shows aggregation, typical for Enchytraeids (O'Connor, 1971). 14 days after the treatment significant density decrease is observed on plot 2 and 3. Compared to the control-plot 1 the compacted plot is marked by a continuous decrease of abundance (up to 90% in June 1979) throughout the investigation period.

A correlation between compaction of soil and decrease in numbers of Enchytraeids on the experimental plot is obvious. Correlation studies between the reduction of Enchytraeids and the volume of macro-pores (>60μ) are in progress.

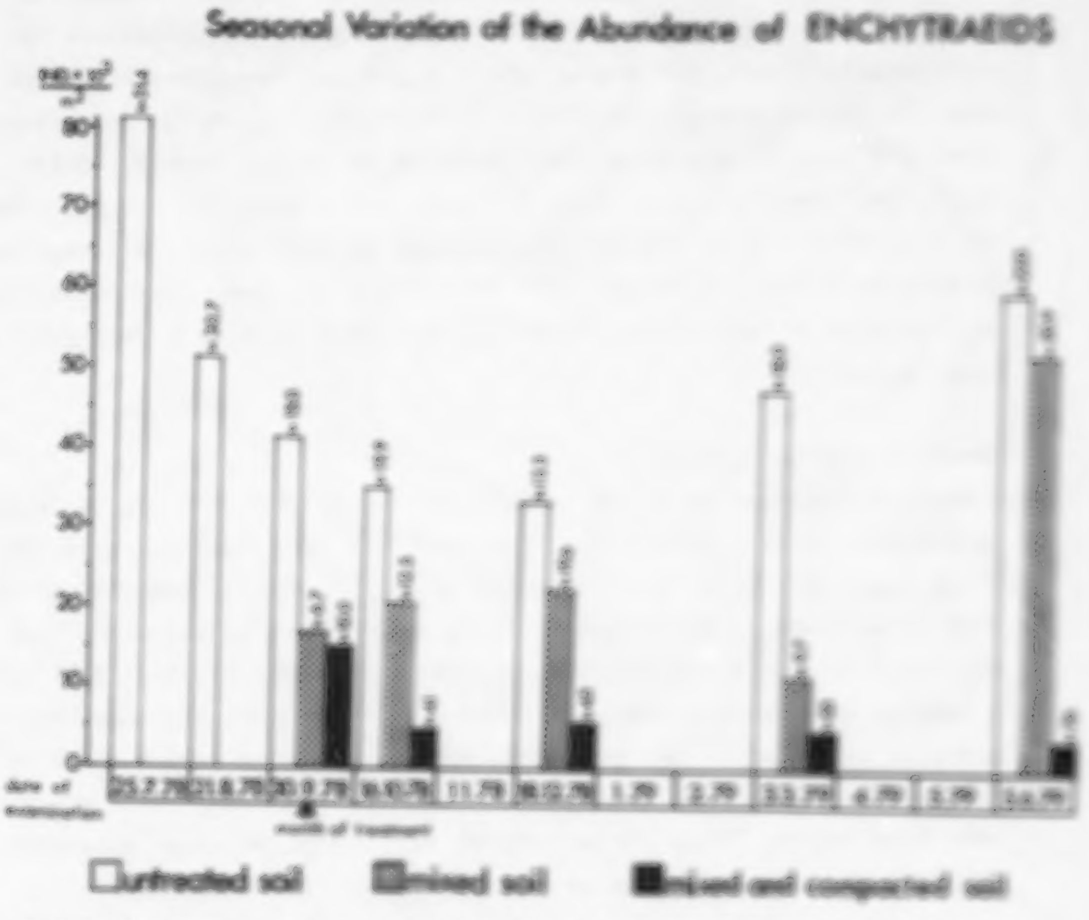

Seasonal Variation of the Abundance of ENCHYTRAEIDS

FIGURE 2: Abundance of Enchytraeidae after different treatment of the soil (mean of 12 samples)

On plot 2 the original abundance has nearly been reached 9 months after the treatment. High precipitation and high soil humidity during the study period (Sept. 78 - June 79) as well as an increase of soil pores > 50 µ for about 55 % has promoted the fast regeneration of Enchytraeids. The usual dry summer months with rapid evaporation of water from the bare soil surface and the high soil temperature on the treated plots may cause additional negative effects on the remaining fauna. Further comparative investigations on the terrestrial invertebrates will be of high interest for the problem of recultivating refuse tips. In such places the abiotic and biotic conditions in general are even worse than on the described test sites.

Comparison of the soil mesofauna of a dump with an adjacent meadow with special reference to Acari and Collembola (prel. rep.)

Introduction

One of the problems concerning the recultivation of waste disposals is the relatively undeveloped soil fauna of the cover. The colonization from the surrounding habitat is controlled by the physical soil conditions and by the dispersal power of the colonizing species. For a zoological soil diagnosis mites are very useful, since their abundance is enormous (up to 2 x 10^5 ind/m^2 in the studied grassland) (Strenzke, 1952).

Research site and methods

A marshland clay grassland adjacent to a dump near Bremen, Fed.Rep.Ger., has been investigated since Feb. 1978 monthly. A simultaneous study on both sites, dump and meadow, started in June 1979. Generally, 12 samples of 20 cm^2 surface and 15 cm depth were taken and cut into cylinders 5 cm deep (100 cm^3). These samples were treated in a modified MacFadyen Canister Extractor (MacFadyen, 1961), 6 days in humid regime (up to 35°C), the following 6 days in dry regime (up to 60°C). The organisms are collected in picric acid and then transferred to an alcohol-glycerin mixture ([illegible], [illegible]), for counting under a binocular microscope.

The abiotic data are from June 79, the biotic data from June 78 (meadow) and June 79 (dump).

Results and discussion

The characteristics of the two sites are:

Grassland: full vegetation cover (Alopeccurus pratensis, Festuca rubra), well developed humus, high percentage of clay (sand ~ 15 %), high moisture (~ 50 %), low pH (4.0 - 4.5). Refuse site: well developed pioneer vegetation (Cirsium arvense, Artemisia vulgaris, Tanacetum vulgare, Poa div. spec.), little or no humus, sand with some clay, low moisture (< 15%), medium pH (6.8 - 7.3).

As shown in table 1, the abundances especially of the Acari differ strongly on both sites.

Tab. 1: Abundances (ranges) of Acari and Collembola of meadow (June 78) and dump (June 79); ind/m^2 x 10^3, o-15 cm depth.

	Meadow	Dump
Acari	168.4 - 1837.6	4.4 - 72.8
Collembola	60 - 119.2	7.6 - 70

In the meadow, the abiotic conditions are very favorable for oribatids (Strenzke, 1952). Here they represent nearly 60% of the mite community. On the disposal site, however, oribatids in addition to being slow colonizers find suboptimal abiotic conditions, which is reflected by their low abundances (Karg, 1962b, 1967; Fig. 4). Gamasids and Tyroglyphids, both highly mobile species with high dispersal power through phoresy make up the major fraction of the Acari community (Stammer, 1962). A predator-prey relationship between these two groups has been suggested by Karg (1961).

The trophic structure of the Acari and Collembola communities of the two investigated sites are very similar. The relative abundances of decomposers (Collembola and mites without Gamasids) in relation to predators (Gamasids) are comparable (meadow: 87/13, dump: 85/15, Fig. 5). This suggests that the two years old plot on the dump has recovered a certain stability. Further studies on the structure of the communities are under progress.

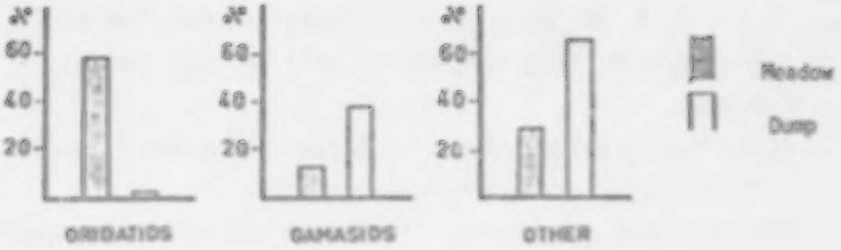


Fig. 4: Composition of the mite communities of meadow and dump.

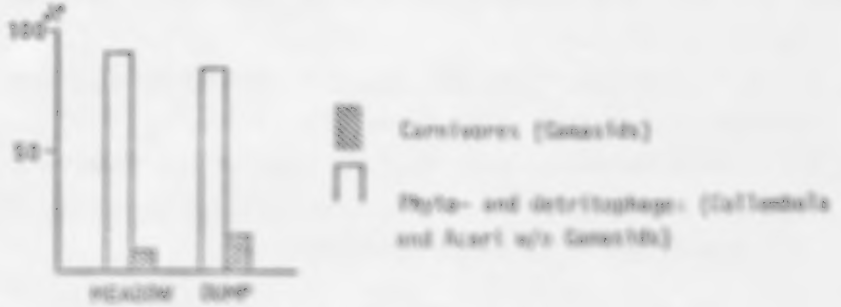


Fig. 5: Trophic structure of the acari-collembola community of meadow and dump.

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SESSION III: ANTHROPHILIC RELATIONSHIPS OF SOIL ORGANISMS

Moderator: Arlan L. Edgar

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PHYSIOLOGICAL AND ECOLOGICAL ASPECTS OF THE COSMOPOLITAN OPILIONID, *Phalangium opilio*

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INTRODUCTION

The daddy longlegs *Phalangium opilio* L. is probably the best known member of order Opiliones (= Phalangida). It was known to Aristotle, mentioned by Robert Hooke and was the only opilionid species named by Linnaeus (Savory, 1962). Many medieval naturalists made recognizable illustrations of it. The species has been recorded from many parts of Europe, North and Central Asia, Asia Minor, North Africa and North America (Spoek, 1963). Forster (1947) reports that it is the only non-endemic opilionid in New Zealand. Indeed, one may conjecture that this was the species that prompted the common names "harvestman" and "reaper" of the group in England and France, respectively. The most descriptive name, daddy longlegs, possibly was given to *P. opilio* in America although common woodland species of *Leiobunum* have longer legs and smaller bodies and also may be the basis for this term.

Perhaps the main reason for our familiarity with *P. opilio* is its occurrence around mans disturbance of nature. Typical habitats include roadsides, fence rows, lawns, gardens, edges of fields and foundations of buildings (Clingenpeel and Edgar, 1966; Sankey and Savory, 1974). These relatively exposed locations are not used ordinarily by other opilionids except by a few long-legged forms in mating season and occasional populations of *Opilio parietinus* (De Geer) in late fall.

The majority of species in any opilionid fauna are under some kind of cover. They may be in forest shade, near the ground under a vegetative overlayment, in fallen litter interstices or in the soil. Why then is *P. opilio* different? Why is there little overlap in the habitats of *P. opilio* and virtually all others?

LIFE HISTORY AND DEVELOPMENT

Most woodland opilionid species reach adulthood in late summer, then mate, oviposit and die in the fall. A few mature in early summer and produce eggs that hatch in the fall. In the former, the species pass the winter as eggs while the latter overwinter as immatures. In both cases there is one generation each year. *Phalangium opilio* exhibits a third pattern. Wintering over occurs both as eggs and immatures. Hatching occurs in the spring and also in mid summer when the winter juveniles reproduce. Oviposition is done both in mid summer and in late fall. Thus mature adults may be seen during a large portion of the summer and fall in temperate latitudes since two populations of adults are produced each year.

Phalangium opilio is more noticeable in the fall than any other time. When man is preparing shrubs and perennials for winter, harvesting crops and garden produce in anticipation of frost P. opilio adults are fully mature. They exhibit considerable movement; mating behavior is easy to observe. Clutches of yellow eggs may be encountered under rocks and solid debris at building foundations and vegetative borders. The cue of declining seasonal temperatures apparently stimulates the species to mate and oviposit.

Egg development requires a cold diapause in several species (Holm, 1947). Without it Opilio parietinus development goes to the blastoderm stage and stops. Embryonation of P. opilio eggs proceeds at a rate controlled by temperature but without the necessity of a cold period. As a consequence, it can be considerably more exploitative of its environment than diapausal species. P. opilio is able to utilize favorable environmental conditions to maximize population size.

Opilionid eggs are very susceptible to dessication and fungal attack. Eggs whose development has been terminated both by evaporative fluid loss and mold colonization have been recovered in nature. Any phalangid species that withstands a broader moisture regime during egg development will have a reproductive advantage. In laboratory incubations, P. opilio eggs have tolerated greater relative humidity fluctuation and resisted mold growth more successfully than the woodland species, Leiobunum longipes Weed, found frequently in contiguous habitats. Eggs of the two species incubated side by side in the laboratory reacted differently at both very high humidities and low ones. Yuan and Edgar (unpublished) observed that eggs of P. opilio develop and hatch with greatest success in an atmosphere of 54 to 90% RH. Klee and Butcher (1968) hatched P. opilio eggs on a substratum of styrofoam in 1/8" dia. holes approximately 1/4" deep in an atmosphere of 75-90% RH. The relative humidity around the eggs probably was much higher, however, since the styrofoam blocks were "kept moist".

Young P. opilio survive more successfully in laboratory cultures than do other species. The general hardiness of eggs and young of P. opilio, along with the life history characteristic of several stages of development in a population at all times, appear to be major factors enabling this species to survive the disturbance of man.

HABITAT ANALYSIS

The open, relatively exposed habitat of Leiobunum vittatum (Say) is as similar to that of P. opilio as may be found in the Great Lakes Region. Leiobunum vittatum is widely distributed in the northeastern United States. The spectrum of environments where it has been found ranges from the trunks of Populus growing in sand dunes to the edge of a quaking mat bog. It apparently adapts readily to new conditions and tolerates severe physical extremes. This species frequently inhabits vegetative borders and ecotones from dense forest to open fields where there is exposure to sun and relatively free air movement; however, it is not abundant around man's disturbance. Of all the non-anthrophilic opilionids it occupies a habitat most like that of P. opilio in terms of temperature, light and relative humidity. For this reason the habitat of P. opilio is compared with that of L. vittatum and occasionally, for contrast, with woodland species of Leiobunum and with a sometimes companion of P. opilio, Opilio parietinus.

In order to explore the habitat preference as well as the vertical distribution of the various opilionid species, a number of localities were visited and at each locality, organisms were collected at three separate strata (ground layer, understory, uppercanopy). For each stratum at each locality, both the abundance of organisms and the density of cover were estimated on a scale of 1 (sparse) through 5 (dense). Thus, after sampling was complete, it was possible to compare the relative abundance of the opilionid species in relation to the cover density in each of three height strata. The abundance-cover profile (Figure 1a) attempts to combine a visual estimate of both the relative abundance of the opilionid species and the density of its associated vegetative and other shade producing cover (Edgar, 1971). Data from 42 sites are combined in Figure 1a. A weighted percentage abundance of organisms in each vegetative strata is plotted versus increasing cover density (sparse = 1; dense = 5). Details of how the percent abundance was weighted and of the other calculations may be seen on p. 41 in Edgar (1971).

Dense grass, other ground layer vegetation and foundations of buildings, support the highest populations of P. opilio. The sum of abundance-cover densities 3, 4 and 5 in ground layer accounts for 86% of total. In other strata, P. opilio is high when shrubs and brushy vegetation are very sparse (1+2 = 96%). The characteristic upper canopy seldom is dense to moderately dense (1+2 = 76%) when supporting high populations of P. opilio. In the majority of instances there are no trees (1 = 53%) present where P. opilio is in greatest abundance (Figure 1a).

The habitats of most opilionids can be characterized not only by density of vegetative cover but also by dominant tree species of the upper canopy. For P. opilio the unusual categories "buildings," and "grass" need to be added. Figure 1b indicates that buildings were the most frequent dominant "upper canopy" in 43% of the sites where P. opilio was collected. Maple and elm canopies were dominant but less frequently so. Above average abundances of P. opilio were encountered in aspen, grass and around buildings. This species was never or seldom collected in several dominant canopy species. Since very few collections of P. opilio were made where aspen was the dominant upper canopy this high abundance value may be considered mainly the result of small sample size (Figure 1b).

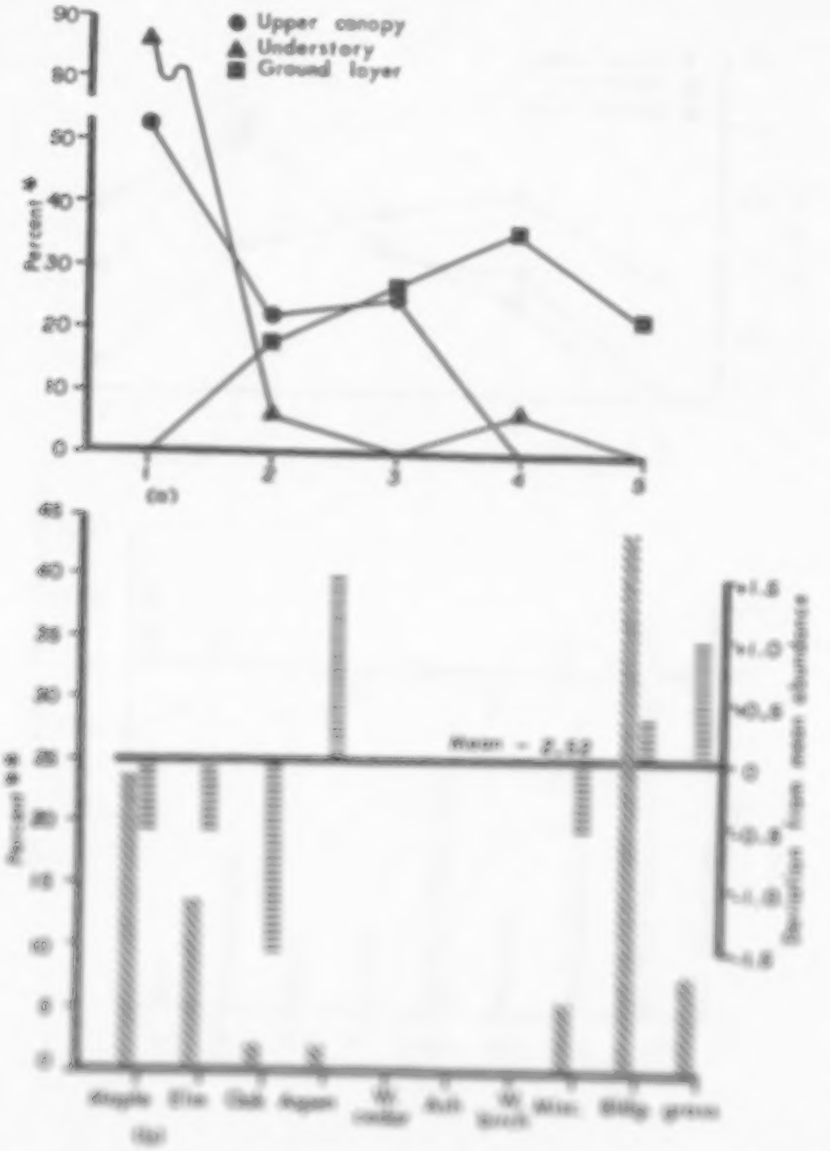

FIGURE 1a & b. (a) Abundance-cover profile plotting weighted percent abundance of *Phalangium opilio** versus increasing cover density (1 = sparse; 5 = dense), and (b) Relative occurrence and abundance of *Phalangium opilio* in the major canopy groups. Understory cover, when associated with buildings was assigned a value of 1. **Percent of collection sites. (Modified from Edgar, 1971)

By comparison the habitat in which Leiobunum vittatum (Figure 2a and b) is most abundant is characterized by moderately dense to dense upper canopy (3+4+5 = 80%) and ground layer vegetation (3+4+5 = 86%). Understory is sparse (1+2 = 46%). All groups of dominant canopy species are colonized by L. vittatum (Figure 2b) with no group supporting a population density clearly greater than any other group.

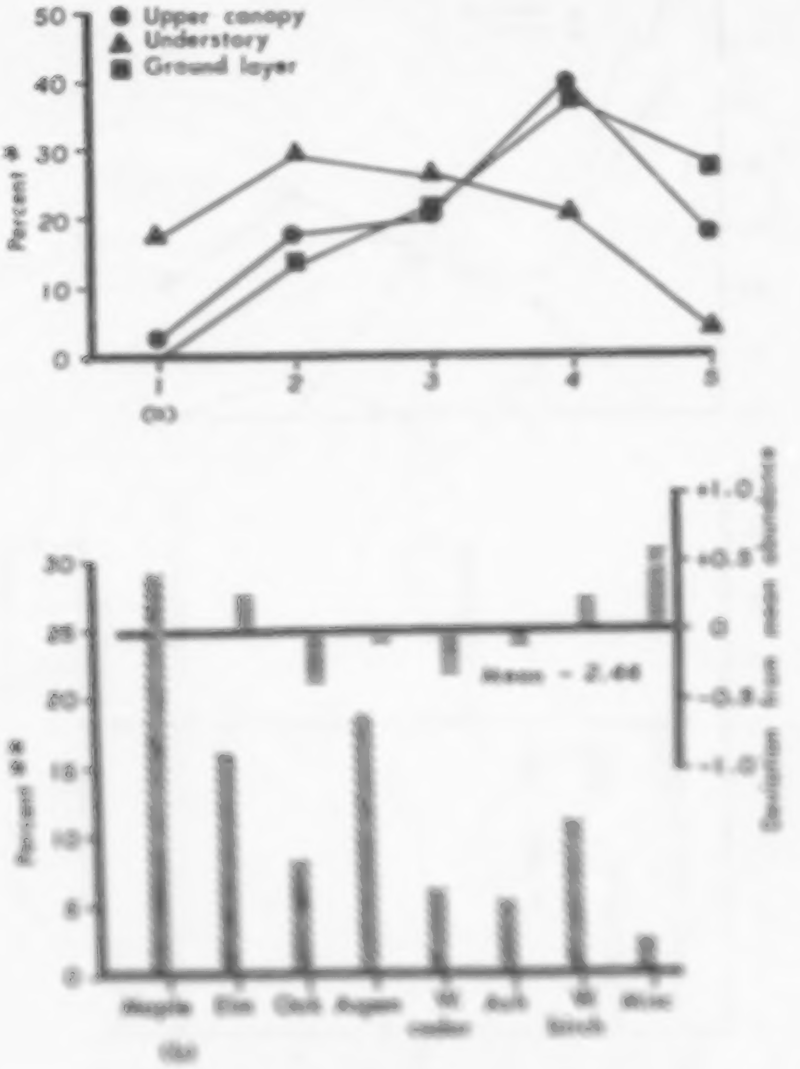

FIGURE 2a & b. (a) Abundance-cover profile plotting weighted abundance of Leiobunum vittatum* versus increasing cover density (1 = sparse; 5 = dense), and (b) Relative occurrence and abundance of Leiobunum vittatum in the major canopy groups. **percent of collection sites. (Modified from Edgar, 1971).

The abundance-cover profile of the forest opilionid, L. longipes shows how comparatively protected it is from moisture and light extremes (Table 1). Leiobunum longipes has a three strata total of 267 (300 possible) as compared with 220 for L. vittatum and only 122 for P. opilio. This suggests that shade is dense and the soil is at least mesic to support this density of vegetative cover where L. longipes is most abundant. The non-anthrophilic, ecotonal L. vittatum is found most abundantly in close proximity to rather dense vegetative cover. The anthrophile, P. opilio, has a stratal total dramatically lower than both L. vittatum and L. longipes.

TABLE 1. A comparison of habitats of three opilionids using cover-abundance profiles of Edgar (1971)

	1) Species, 2) Association with man and 3) Habitat		
Stratum	1) Leiobunum longipes* 2) Non-anthrophilic 3) Protected	Leiobunum vittatum Non-anthrophilic Ecotonal	Phalangium opilio Anthrophilic Exposed
Upper canopy	3+4+5 = 97	3+4+5 = 80	3+4+5 = 24
Understory	3+4+5 = 96	3+4+5 = 54	3+4+5 = 14
Ground layer	3+4+5 = 74	3+4+5 = 86	3+4+5 = 84
	267	220	122

*Edgar, 1971, Figure 6, p. 44

On the basis of habitat analysis alone P. opilio and L. vittatum might be expected to be more able to withstand environmental extremes than L. longipes. Further, P. opilio should have additional physiological and/or behavioral attributes over L. vittatum to exist successfully in its physically harsher environment.

PHYSIOLOGICAL ECOLOGY

Light selectivity

In a light gradient both male and female P. opilio occupy a zone of higher intensity than two other opilionid species (Figure 2), Leiobunum politum Weed and L. vittatum, which are found in habitats contiguous with that of P. opilio in Michigan ([illegible] and Edgar, [illegible]). The order of dark-to-light preference is predictable on the basis of the usual habitat of each species. The habitat of L. politum is typically denser and supplied with a more constant source of moisture than

L. vittatum, and likewise, L. vittatum occupies a more protected position in relationship to sunlight than does P. opilio.

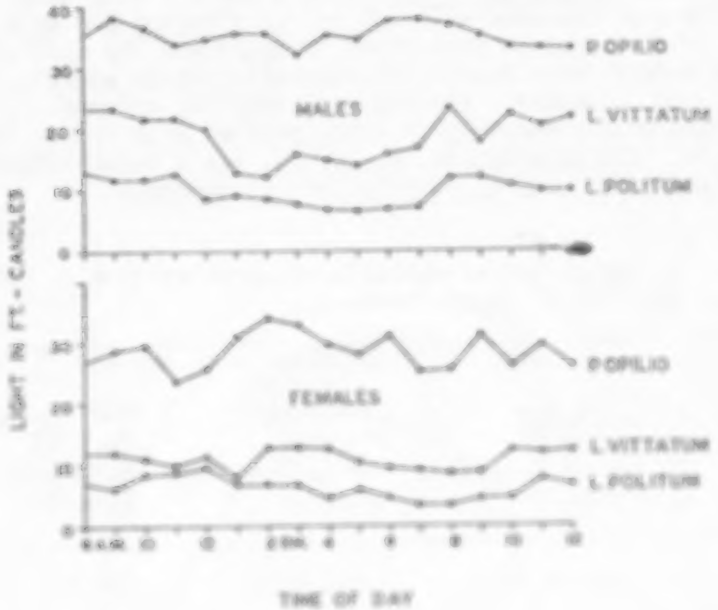

FIGURE 3. Light intensity preference of three species of phalangids in a light gradient. Dots indicate the location of individuals in a light gradient.

In nature, males are generally more conspicuous. This is borne out in the laboratory gradient by the fact that the males of all three tested species generally were found in a higher light intensity than females (Figure 3).

From these data there appears to be no consistent reaction to light on the basis of time of day. However, another study (Edgar and Yuan, 1968) indicated that there is more activity by both sexes of P. opilio during dusk and darkness and relative inactivity in daylight (Figure 4). Periods of virtually no activity closely parallel times of the day when light intensity is the greatest. Ninety percent of total activity occurred between 6 p.m. and 6 a.m. In its natural, relatively exposed habitat this activity pattern should allow P. opilio maximum conservation of body moisture since it avoids daily temperature extremes and is most active when ambient humidities are the highest.

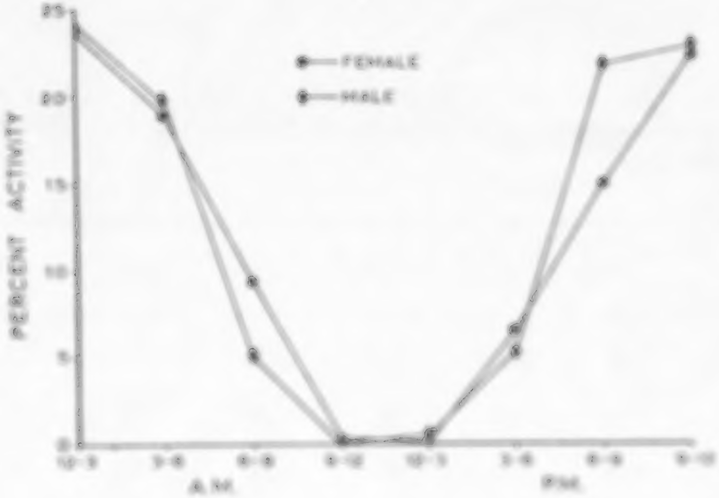

FIGURE 4. Averaged activity of *Phalangium opilio* in normal light.

The general pattern of inactivity during daylight and activity during darkness is seen in several species of *Leiobunum* and *P. opilio* (Edgar and Yuan, 1968). Activity was measured in the laboratory by tallying the number of times the animal walked the length of an activity chamber. During periods of activity, approximately 6 p.m. to 6 a.m., *P. opilio* is conspicuously more active than all seven species of *Leiobunum* tested (Table 2). It travelled 25 times more distance than the ecotonal *L. vittatum* and forest *L. longipes*. This considerably elevated activity level suggests that *P. opilio* does not have to depend on immobility and seclusion for protection against its enemies but rather can move about more freely in search of food, mates and protection from the deleterious aspects of its physical environment.

TABLE 2. Comparison of mean total activity per day by *Phalangium opilio*, and seven species of *Leiobunum* in normal light. (Modified from Edgar and Yuan, 1968)

	P.o.[1]	L.ni[2]	L.c.[3]	L.ve.[4]	L.np.[5]	L.p.[6]	L.vi[7]	L.l[8]
♂	567*	449	109	26	40	31	17	17
♀	555	317	58	54	16	13	28	27
Mean	561	383	83.5	40	28	22	22.5	22
Activity Ratio	25.5	17.3	3.8	1.8	1.3	1	1	1

1 *Phalangium opilio*, 2 *Leiobunum nigripes*, 3 *L. calcar*, 4 *L. ventricosum*, 5 *L. nigropalpi*, 6 *L. politum*, 7 *L. vittatum*, 8 *L. longipes*

*Number of trips from one end of chamber to the other for all individuals tested.

Relative humidity and survival in dry air

Opilionids in a humidity gradient appear to select higher humidities after a short period of orientation (Todd, 1949; Clingenpeel and Edgar, 1966). Few species have need of a particular relative humidity within 12 to 15 hours of deprivation from food and water. As time passes and body water is depleted, they appear more sensitive to moisture levels in the air and this is expressed by movement into higher humidities (Edgar, 1971).

Comparative survival in a humidity gradient should indicate something about both the hardiness of a species to withstand the extremes in its environment and hardiness in relationship to other species tested. In this respect *P. opilio* is comparable to *L. vittatum* and both are much more tolerant to desiccation than *L. politum* (Clingenpeel and Edgar, 1966).

An extension of this measure of comparative hardiness is survival in dry air. Adults of both sexes placed in desiccation chambers live varying periods of time. Rate of loss of water, and percent loss of body weight are factors which affect survival time. The animals surviving longer lose water slower and/or are able to withstand greater weight loss before death. Among four species of *Leiobunum*, including *L. vittatum* and *L. politum* referred to earlier, *L. vittatum* survived more than twice as long as the other three; *P. opilio* survived 13% longer than *L. vittatum* (Edgar, 1971) (Table 3). Considering all three criteria, survival time, percent body weight loss and rate of body weight loss, P. opilio out performed the four Leiobunum species tested on all counts except one (female L. vittatum lost body weight slightly slower than female P. opilio).

TABLE 3. Response by five opilionid species in dessication chambers (modified from Edgar, 1971)

Species	Survival time (hrs.)		Body wt. loss[1] (per cent)		Rate of body wt. loss (%/hr.)	
	♂	♀	♂	♀	♂	♀
L. politum	18.4	38.6	40.0	44.6	2.76	1.36
L. longipes	25.1	59.1	36.7	38.1	1.67	0.83
L. calcar	37.0	47.5	43.5	45.6	1.33	1.0
L. vittatum	56.4	116.1	43.7	48.9	0.81	0.48
P. opilio	75.6	120.0	48.3	57.6	0.72	0.52

1 calculated at time of death.

Temperature tolerance

Given access to a range of temperatures, opilionids might be expected to spend the most time in a narrower range that represents conditions they encounter in nature. Results obtained from several species having access to a temperature gradient for a period of several hours appear to bear this out (Figure 5). Six opilionid species in such a situation show mean values which appear to accurately reflect the degree to which they are exposed to temperature influence from the sun and evaporative cooling. The mean temperature values for Leiobunum vitattum and P. opilio were substantially higher than three woodland species of Leiobunum and suggest that both are well adapted to higher summer temperatures. In contrast, O. parietinus is often found on the shaded side of cement walls where usually the humidity is high and the substrate is cool. Its mean temperature preference of 19.7°C is to be expected and lends further authenticity to the temperature mean for P. opilio.

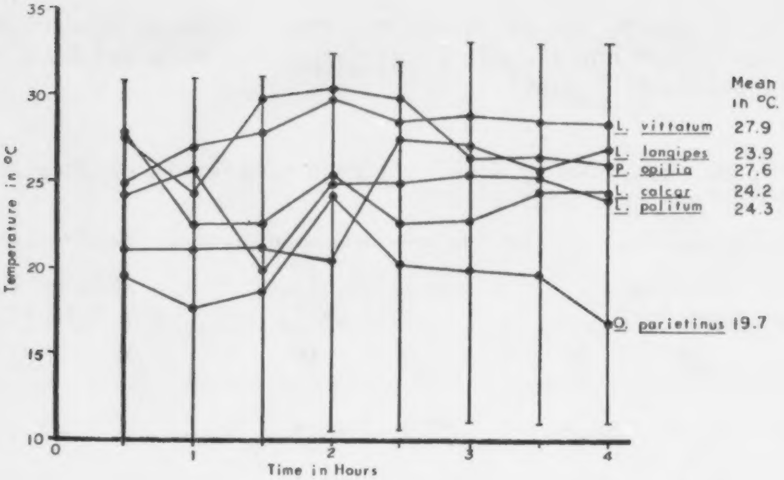

FIGURE 5. Mean temperature preferences of six species of phalangids, based on location in a temperature gradient at successive half-hour intervals. Limits of gradient are indicated by cross lines at ends of time bars. Each point is the mean of 3-5 values (from Edgar, 1971).

SUMMARY

Phalangium opilio has been reported from widely separated regions of the world and probably is the best known species in order Opiliones. It is anthrophilic, being associated with mans disturbance in gardens, lawns, roadsides, building foundations and fields. The occurrence of other opilionids around man probably is incidental to their search for food, shelter or mates.

More than one life history stage of P. opilio exists at a time and the eggs develop to hatching without a cold diapause. Both eggs and young are more hardy than other species in laboratory manipulations.

Compared with that of associated opilionids the habitat of P. opilio is more exposed to broad extremes of light intensity and moisture. The density of vegetative cover is low. Trees seldom are as important as grass and buildings for shelter.

In laboratory experiments involving light, water and temperature the performance of P. opilio matches what would be predicted on the basis of the natural environment of the species. It chooses higher light intensities and temperatures, survives longer in dry air and moves about more than associated species.

Phalangium opilio appears to be well adapted for survival around man.

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QUESTIONS and COMMENTS

M.S. GHILAROV: In what meaning do you use the term "survive desiccation" - ability to lose water and survive, or being protected from water loss. (According to my and L.M. Semenova's data the epicuticle of Ph. opilio is very thick especially on tergites).

A.L. EDGAR: I don't have histologic data to indicate exoskeletal thickness or waxiness of the cuticle. In fact, the question could be asked whether death occurs from desiccation (water loss) or from suffocation. The answer to that is likewise not known specifically for the opilionids tested.

ACTIVE AND PASSIVE DISPERSAL OF LUMBRICID EARTHWORMS

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INTRODUCTION

Gates (1972), through the cooperation of the United States Bureau of Plant Quarantine, accumulated considerable evidence to support his hypothesis that the lumbricid fauna of northern North America represents principally species introduced there and distributed within the continent by man. Of the 3400 earthworm specimens seized by inspectors from imported plants during a 15-year period, nearly 1600 were lumbricids, representing 16 species. Because many of these species, in addition to other lumbricids, are holarctic or even "cosmopolitan" (*sic* Gates 1972) in distribution, it is easy to follow Gates' (1970, 1972, 1976*a*) reasoning that the present range of each reflects their transport to other regions by man. For North America, alone, Gates (1976*b*) lists 24 lumbricid species as "exotic," the source continent of most of these lumbricids presumably having been Europe; transport to North America was probably accidental, such as earthworms trapped in ship ballast or among the roots of imported plants.

In North America today, the dense distribution across the continent of many of these "exotic" lumbricids (*e.g. Lumbricus terrestris* L., *L. rubellus* Hoffmeister, *Aporrectodea* spp., *Octolasion* spp., and others) precludes the determination of the place(s) and time(s) of their introduction. Indeed, fossil evidence (Schwert 1979) indicates that at least one of these widespread "European exotics," *Dendrodrilus rubidus* (Savigny), was inhabiting North America over 10 000 years ago, certainly well before the arrival of European settlers. The limited distribution of some other "exotic" lumbricids in North America, however, clearly indicates the general region, if not the exact time, of their introduction to this continent. A population of the European lumbricid *Aporrectodea icterica* (Savigny), now well established in the region of an arboretum in southern Ontario, Canada, probably originated from trees imported to the site from England in 1971 (Schwert 1977). The limited distribution, outlined by Reynolds (1976) of *Lumbricus festivus* (Savigny) within the Saint Lawrence watershed of eastern North America, appears to represent a species introduced to that region in one or more isolated localities decades or perhaps centuries ago and since slowly expanding its range outward from the valley.

Unfortunately, Gates and others have probably relied too much on man as the agent responsible for the present lumbricid distribution in northern North America. Certainly while being a major, if not the primary, influence on earthworm distribution, man cannot claim responsibility for the total distribution. We now know that endemic earthworms, including geophagous species, often densely inhabit the northern Appalachians and even some deglaciated areas of the continent; given so many thousands of years since deglaciation "to eat their way" (*sic* Gates 1976*a*) over these mountains, it is not surprising to find the endemic lumbricids *Bimastos* or *Eisenoides* throughout the state of Pennsylvania and even into New York and Massachusetts.

The seemingly sedentary nature of earthworms is misleading. In northern North America, most lumbricids are remarkably active throughout the spring and autumn, and, in the southern regions, winter. Whether one accepts or rejects Gates' premises on their present distribution, the wide and dense distribution of many of these species across North America have benefited from their extraordinary abilities at natural dispersal. Of the three to be mentioned, one is an active mechanism, while the other two involve passive dispersal through other natural agents. All three are in need of further investigation, and additional mechanisms probably exist.

STREAM DRIFT

The moist lowlands adjacent to streams and lakes are often ideal habitats for many species of Lumbricidae. Significant activity of these earthworms at or near the surface occurs when temperature, moisture, and light conditions permit. Inevitably, many individuals are washed into these waterways from surface runoff resulting from rainfall and snowmelt or from mass movements of soil during erosion, and they can potentially be transported long distances downstream. Bouché (1972) noted that several species of earthworms inhabit only particular drainage basins in France and hypothesized that stream drift was probably an important factor in influencing their distribution. Ward (1976) applied a similar hypothesis to explain the recolonization of a riffle area by the lumbricid *Eiseniella tetraedra* (Savigny) in a Colorado stream. Although adult lumbricids can remain submerged in aerated water for prolonged periods (Roots 1956; Edwards and Lofty 1972), the mortality rate of individuals must be high during stream transport due to predation and physical battering. Nevertheless, live lumbricids can be frequently seen on stream bottoms, and the potential value of this drift to the dispersal of the species involved must be considerable.

During an analysis of a small stream in southern Ontario, Canada, Schwert and Dance (1979) recovered over 300 lumbricid cocoons from drift samples. Of the total, 92% were found to contain sperm and albumen or some stage in the development of the embryonic mass; these were believed, therefore, to be viable and potentially capable of hatching. From identification of the cocoons, they were found to represent at least six genera of Lumbricidae, all of them common to that region.

The small size and tough, spheroidal outer walls of these cocoons are, unlike the adult worms, ideally suited for long and rigorous transport downstream. Their palatability to fish is unknown, but presumably low. Roots (1956) demonstrated that cocoons, such as those of the lumbricid *Allolobophora chlorotica* (Savigny), could successfully hatch while submerged, with the young also undergoing normal growth in a submerged environment. From the remarkably high viability of the stream drift cocoons, their successful hatching could, likewise, be expected in areas of a stream where the cocoons had been deposited near the margin or in the bottom sediments of pools. Consequently, these transported species would become established in lowland areas downstream of their original source.

Since this study, numerous cocoons have been isolated from other streams in Canada and the United States, and this phenomenon appears to be widespread. Further investigation, however, will be needed to determine the degree in which such dispersal may have actually influenced lumbricid distribution.

MASS EMERGENCE

In northern North America and Europe, the mass emergence of lumbricids during periods of heavy rainfall or dew is a common, yet poorly studied, phenomenon. Such emergences were first described by Darwin (1881) and were subject to casual analysis by Friend (1924). Because this occurrence is more often witnessed in areas affected by human civilization, the deaths of often hundreds of thousands of individuals stranded on drying streets and sidewalks have led to popular conceptions that the dying earthworms were ill, poisoned, or drowned. Lankester (1921), Merker (1926, 1928), Nishida (1951), and others, in search of a more scientific explanation, proposed that through chemotaxis the worms are forced to the surface as the oxygen supply to the soil is cut by rain saturation; Shiraishi's (1954) experiments failed to demonstrate this. Doeksen (1967) proposed that similar types of "migrations" observed in wet, foggy greenhouses result from behavioral changes in the worms resulting from increased hydrogen sulphide concentrations in the soil. Svendsen (1957), without seeking a chemical factor to explain surface activity, proposed that some species actively search for food sources during rain; in his experiments, he noted that several lumbricid species aggregated to dung through movements at or near the surface during moist conditions.

However precipitation actually triggers such surfacing, these mass emergences are so predictable in occurrence and so massive in scope, usually affecting several species at one time, that an additional hypothesis may be proposed with respect to the following two points:

1) Mass emergences occur primarily during periods of cool, moist weather. Friend (1924) noted emergences in England occurring only during the autumn, winter, and spring months. In North America, soil temperatures taken at a 3-cm depth during emergences in Ontario, Canada and in North Dakota, U.S.A. have ranged from 2° to 9° C. When soil temperatures rise above this range, as in the summer months, this phenomenon rarely occurs. A notable exception to this behavior is *L. terrestris*, which is known to surface for food and mating throughout the summer months.

2) Before human civilization, the original habitats of the Lumbricidae were primarily forests and forest meadows. Unfortunately, as previously noted, most observations of mass emergences have been in urbanized areas, where the earthworms are trapped by man-made structures and quickly killed by desiccation and sunlight. This surfacing phenomenon, however, also occurs on the forest floor, where the surfaced individuals are protected from desiccation, sunlight, and large predators by the tree canopy and by litter cover. During periods of cool litter temperature and sufficient moisture to permit respiration, the lumbricids may enter the litter and migrate through it rapidly and for long distances without the need to burrow. Contrary to popular belief, surfaced individuals can rapidly re-enter the soil in areas where it is sufficiently porous.

With this combination of proper soil temperature, sufficient moisture from fresh precipitation, protection from sunlight and predators, and the loose litter medium for enhanced mobility, free and rapid surface dispersal can occur in relative safety. Such a behavioral response is advantageous to the species involved as it: 1) no longer limits the active outward dispersal of geophagous species to burrowing activity; 2) decreases population pressure during periods of peak reproduction and, therefore, food and space competition in areas of high earthworm density; 3) rapidly expands the range of the species involved; 4) enhances the possibility of genetic exchange among scattered populations of a species. The direction of dispersal movement appears to be random, even on sloping surfaces, and inevitably many individuals are washed into streams, potentially to colonize downstream areas.

In northeastern and northcentral North America, nearly all of the established species of *Lumbricus*, *Eisenia*, *Allolobophora*, *Octolasion*, *Aporrectodea*, *Dendrobaena*, and *Dendrodrilus* can be observed surfacing during proper conditions at cool times of the year. Several species of *Bimastos* are, likewise, known to surface. Sub-aquatic Lumbricidae inhabiting saturated environments, such as *Eisenoides lonnbergi* Michaelsen and *Eiseniella tetraedra* are, as would be predicted, unaffected by the precipitation trigger.

TRANSPORT BY OTHER ANIMALS

No published records apparently exist of earthworm individuals or their cocoons accidentally being transported by birds or mammals. Cocoons could be carried substantial distances if trapped in mud on birds' feet. Live individuals carried by predaceous birds are, from observation, occasionally dropped in midflight and could potentially reburrow. Certainly some of the intriguing earthworm records of James R. Philips (unpublished data, personal communication 1973 - 1975), such as immature *Lumbricus terrestris* apparently established in a kestrel (*Falco sparverius* L.) nest positioned on a tree limb 6 m above the forest floor, are attributable to avian transport. Whether such passive transport has profoundly affected earthworm distribution is impossible now to determine; in all probability, it has been of marginal significance.

SUMMARY

Although a number of lumbricid species now inhabiting North America were introduced there by man, human transport cannot alone account for their remarkably widespread establishment across the continent. Rather, many Lumbricidae are capable of rapid dispersal through active or passive means other than by burrowing or by man. Dependent upon seasonal conditions, random movement of some species, often on a mass scale, occurs at or near the surface during periods of rainfall or of heavy dew; atmospheric and soil temperatures appear to be key factors in determining periods and size of such movements. Downslope dispersal of the Lumbricidae is facilitated by stream drift, especially during the cocoon stage in which up to 90% may remain viable after drifting often considerable distances. Avian transport of individuals is a small, but potentially significant mechanism of passive dispersal.

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M.S. GHILAROV: The cause of emergence of earthworms on the surface is the deficiency of O_2 after heavy rains in summer in the soil. In spring after melting of snow earthworms don't emerge on the surface, whereas after spring flooding they don't die off, but after summer floodings of rivers they do perish. These facts were shown still in the 20's by Berclemisher and Chetyrkina. Certainly emergence on soil surface after summer rains allows the active dispersal and mixing of population; this has been stressed already e.g. by Perel and by Kvavadze.

Passive dispersal along slopes by rains is described by Atlavinyte, whereas in arid territories of Central Asia earthworms in natural conditions are known only along river benches (and subsequently along irrigation channels. So previous data of soviet zoologists are in accordance with your conclusions and support them.

A. TOMLIN: There are examples of L. terrestris rising and dispersing after rainfalls in July and August (3 cm soil temperature 12°C) though greatest emergence admittedly occurs April-June and Sept-Oct. I particularly refer to the Windsor Airport situation. I disagree that L. terrestris dispersal is limited to "cool" soil temperatures.

D.P. SCHWERT: Of all the peregrine species discussed, only Lumbricus terrestris regularly feeds on the surface. Surface feeding for this species does occur in mid-summer, when soil temperatures are greater than 9°C. I am surprised, however, at learning of a mid-summer mass phenomenon causing problems at Windsor.

A. CARTER: To what degree does the availability of areas for shelter affect the amount of earthworm movement after heavy rains? In flat grassy areas (city lawns), soil may become readily water-logged and earthworms have no hummocks for shelter.

D.P. SCHWERT: I have no quantitative information on which to answer this question. For reasons that I have just outlined, however, we could expect that the lack of shelter in such areas would lead to proportionally far greater mortality than in forests.

C.A. EDWARDS: You give the impression that the surfacing of earthworms after rain is confined to Lumbricidae in cool weather. It is common in hot weather in the tropics by Eudrilidae and Megascolecidae.

D.P. SCHWERT: I'm aware that other families do surface, however, I am not certain whether the same behavioral response for tropical earthworms is involved.

D. MALLOW: What studies, if any, have been done on rates of movement by lumbricid worms, with regards to their emergences during fall and spring rainfalls?

D.P. SCHWERT: At this time, I know of no such studies. My own research efforts in North Dakota are inhibited by low earthworm densities and limited rainfall in this part of the continent.

HORIZONTAL MOVEMENTS IN A NATURAL POPULATION OF *Entomobrya socia* IN A LAWN

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Horizontal movements within a population, or mixing, are of general interest in both population ecology and population genetics. In springtails in addition to affecting individual activities and population parameters, movements influence the dispersal of microorganisms.

As a part of a study of Entomobrya socia in southern Louisiana, I have examined horizontal movements in a natural population. This epigeic species is accessible for sampling and abundant in lawns composed primarily of St. Augustinegrass (Stenotaphum secundatuni (Walt.) Kunze). Using sticky plates as snares I have captured the animals entering an area of lawn. These data have been compared with estimates of population density obtained by suction sampling at about the same dates.

METHODS

Square plates of plexiglass 25 cm on each side were generously coated with Tanglefoot^{TM}, a fruit tree grease. Placed flat in one area on the lawn, these captured insects that alighted on them. Two experimental designs were utilized. Initially 6 plates coated on both sides were set out at 10 AM. At 4 hour intervals thereafter one was recovered until the last was retrieved at 10 AM the following day. This procedure was followed from mid-April to mid-May 1978. As no Entomobrya were collected on the lower plate surface and more replicates were needed, a second design was substituted. Three plates coated on only the upper surface were distributed, retrieved 2 hours later and 3 new plates set up. To reduce the stimulating effect of disturbance, I did not step closer than 40 cm to a plate. This procedure was followed for 24 hours on six dates from May through mid-July 1978 (Table 1).

Animals captured were counted, the samples from the first procedure pooled, all (700) individuals were measured, and the presence or absence of gut contents (visible through the translucent body wall) was recorded.

For comparison, standard samples were collected with a household vacuum cleaner with a filter fitted over the nozzle. The filter was moved over the wire screen within a wooden frame (19.3 cm X 30.4 cm) to collect a sample. Four sites were sampled between 4 PM and 6 PM on the dates of sticky plate captures or near to them (Table 1). Estimates suggest that this method removes about .7 of the Entomobrya present, that is, it is about 70% efficient. The data were utilized without correction. Animals were measured and the presence or absence of gut contents was determined.

RESULTS

Individuals that moved horizontally were of large body size. Figure 1 depicts the numbers in four size classes with the general population shown below the lines and mixers above. Mixers represented about the upper 50% of the size range of the population present. Large animals dominated even in mid and late June when juveniles were numerous. This suggests that most were adults, and, because female springtails tend to be larger than males, that many were females.

The translucent body of *Entomobrya* in preservative allowed the presence of absence of gut contents to be recorded. In Figure 2 the fractions empty are illustrated by bars with dots for immigrants and bars with slanted lines for the general population. Of the mixers about twice as many had empty guts as animals of the same size from suction samples. As fasting characterized the interval preceding and following ecdysis, the data suggest that many of the immigrants were near the time of ecdysis. For *Tomocerus minor* and *Orchesella cincta*, DeWith and Joosse (1971) found that locomotor activity increases immediately after ecdysis.

TABLE 1. Numbers of *Entomobrya socia* caught on sticky plates and in suction samples. Two standard errors are given in parentheses.

Immigrants			Standard Populations		
Dates	Total on Plates	$\bar{x}$/day in 25x25cm	Suction Sample Dates	Total Catch	$\bar{x}$ per Sample (49,132 mm^2)
15 Apr.	5	1.4	8 Apr.	109	27.25 (25.25)
20 Apr.	9	2.6	23 Apr.	116	29 (9.2)
10 May	38	10.8	9 May	209	52.25 (44.6)
25 May	86	28.7 (3.5)	31 May	576	144 (29.6)
5 Jun.	129	43. (17.6)	5 Jun.	491	122.75 (53)
15 Jun.	64	21.3 (7.8)	13 Jun.	149	37.25 (20.3)
21 Jun.	79	26.3 (8.1)	21 Jun.	334	83.5 (53.4)
1 Jul.	224	74.7 (6.5)	29 Jun.	660	165 (96.5)
18 Jul.	66	22 (2.5)	18 Jul.	299	74.75 (28.1)

The numbers of animals moving horizontally varied with several factors. First, time of day was a determinant producing a daily pattern of movements. For all sample dates there was a bimodal pattern with maximum mixing between 9 to 11 AM and 5 to 9 PM (Figure 3). The two dates (5 June and 1 July) with morning immigration extended to 1 PM were the only two with overcast skies. A diurnal rhythm of horizontal activity has also been described from pitfall trap data on *Smithurides malmgreni*.

FIGURE 1. The body size distribution of animals that moved horizontally (shown above the lines) and the general population (shown beneath the lines). The numbers are the numbers of individuals in each category.

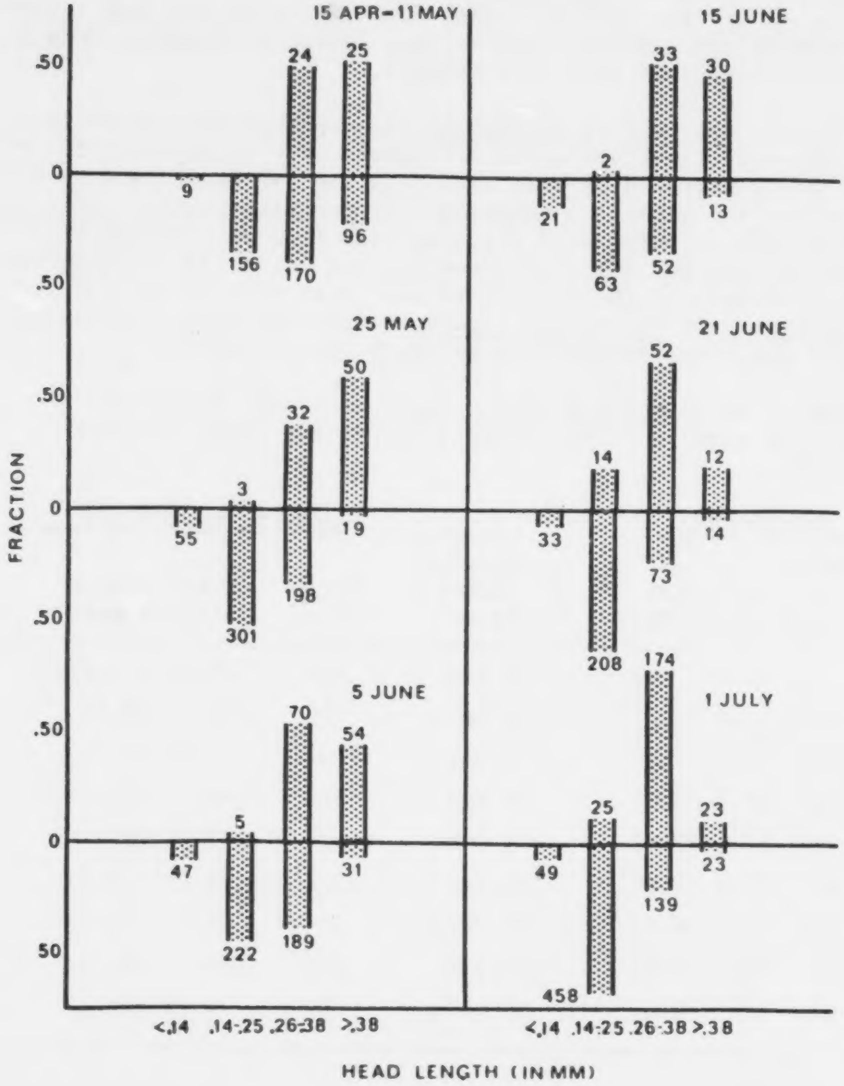


FIGURE 2. The fraction of empty animals among the mixers (shown as bars with dots) and among the general population (shown as bars with diagonal lines). The numbers give sample sizes.

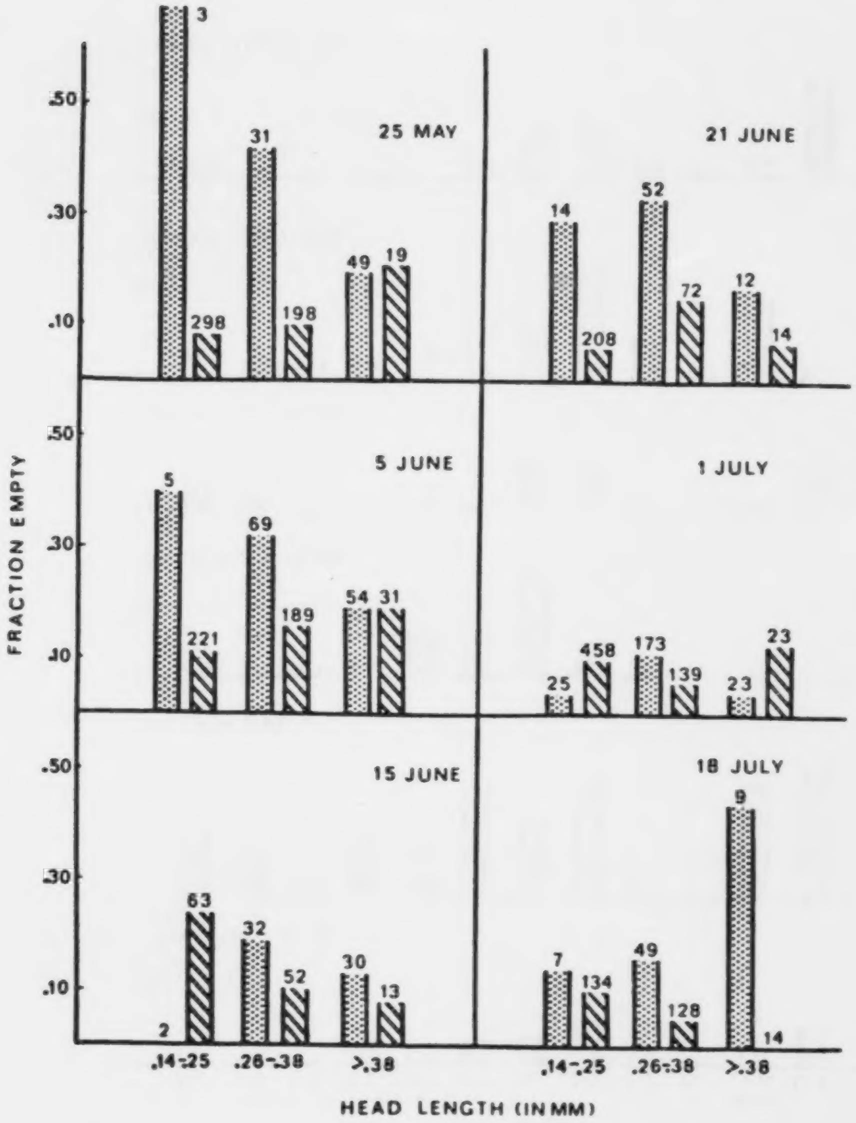
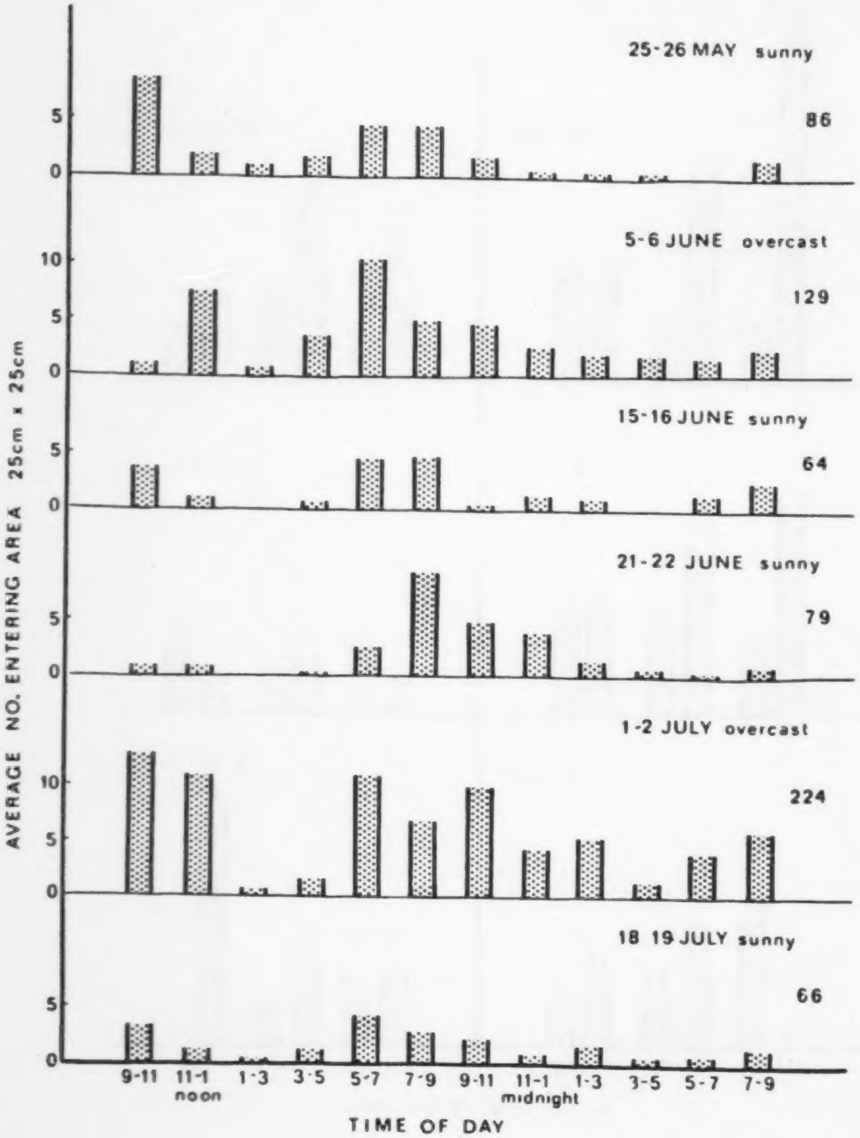


FIGURE 3. The average numbers of immigrants (entering area 25 cm X 25 cm) at various times of day. The descriptive terms refer to cloud cover; the numbers on the right are the total animals trapped on that date.



Working in West Greenland, Kristensen and Vestergaard (1975) found only one peak of activity per 24 hours during the day. Bowden, Haines and Mercer (1976) report that climbing by Collembola above the substrate occurs primarily between 5 PM and 10 AM, an interval that includes both the maxima of _E_. _socia_.

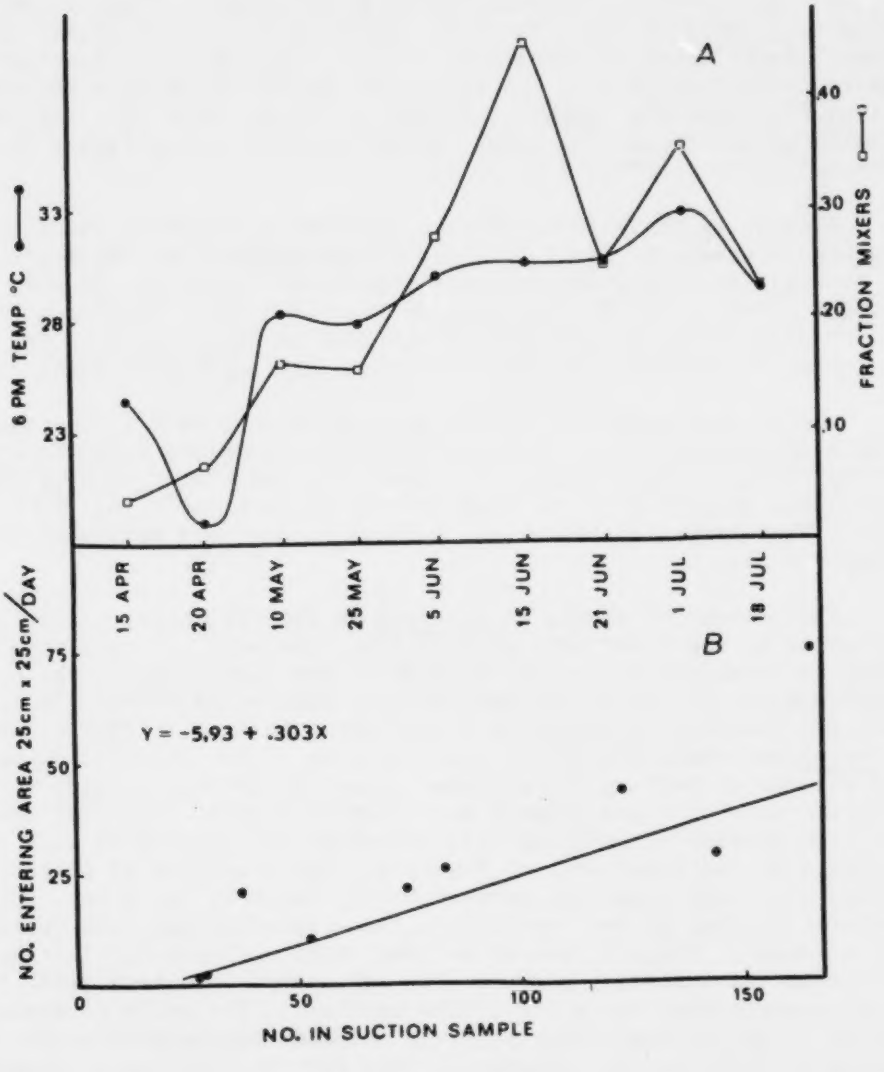
Season, temperature and population density influenced the numbers of mixers per day. Figure 4A illustrates the fraction of the animals present that moved horizontally on different dates. There is an upward trend from April to June. The same figure depicts the 6 PM air temperatures. Temperature is significantly correlated with the fraction of mixers ($r = .7892$; $P = .01$). The points in Figure 4B show the observed relation between the number of mixers on the vertical axis and population density on the horizontal axis. Again there is a significant positive correlation ($r = .8787$; $P = .0018$).

Because as the seasons advance both the temperature and population density increase, it is of interest to determine which exerts the effect on mixing. By a maximum r-square improvement procedure, density was found to account for 77.2 percent of the variation. The linear equation $Y = -5.93 + .303X$, illustrated by the line in Figure 4, best describes the relation between the number of mixers and population density.

The average number of mixers per day (per 25 cm x 25 cm) ranged from a minimum of 1.4 on 15 April (the first sampling date) to a maximum of 74.7 on 1 July (Table 1). These are associated with estimated population densities in the same area of 35 on 8 April and 165 on 29 June. Thus from 4 to 45% of the animals present are estimated to have moved per day.

The pattern of mixing by _E_. _socia_ in the days after rainfall is presented in the upper half of Figure 5. The vertical bars show plus or minus two standard errors of the means. Two significant peaks of mixing follow rainfall. In SE England, Bowden, Haines and Mercer (1976) found that the number of climbers increased after rainfall. Earlier work on _E_. _socia_ has demonstrated the synchronizing effect of rainfall on molting and periods of fasting (unpublished except an abstract; Waldorf, 1978). The fractions of empty animals from suction samples collected through the warm periods of 1978 and 1977 are shown for successive days after rainfall in the lower half of Figure 5. The fractions of pharate animals of the same body sizes are represented by the vertical bars. There are peaks of fasting at two days and at four day after rainfall (Waldorf, unpublished). Since I know of no laboratory evidence for fasting except preceding and following ecdyses (see for example, Thibaud 1968, 1976), this suggests that two molts follow rainfall. The peaks of mixing occuring 1½ and 4½ days after rainfall coincide approximately with the timing of molting. The absence of data for the fraction of mixers at two days and four days after rainfall might account for the differences. The general similarity of these graphs supports the idea that animals mix about the time of ecdyses.

FIGURE 4. A) illustrates 6 PM temperature and the fraction of mixers on successive sample dates. The points in B) represent the relationship observed between number of mixers and general population density. The equation is illustrated by the line.



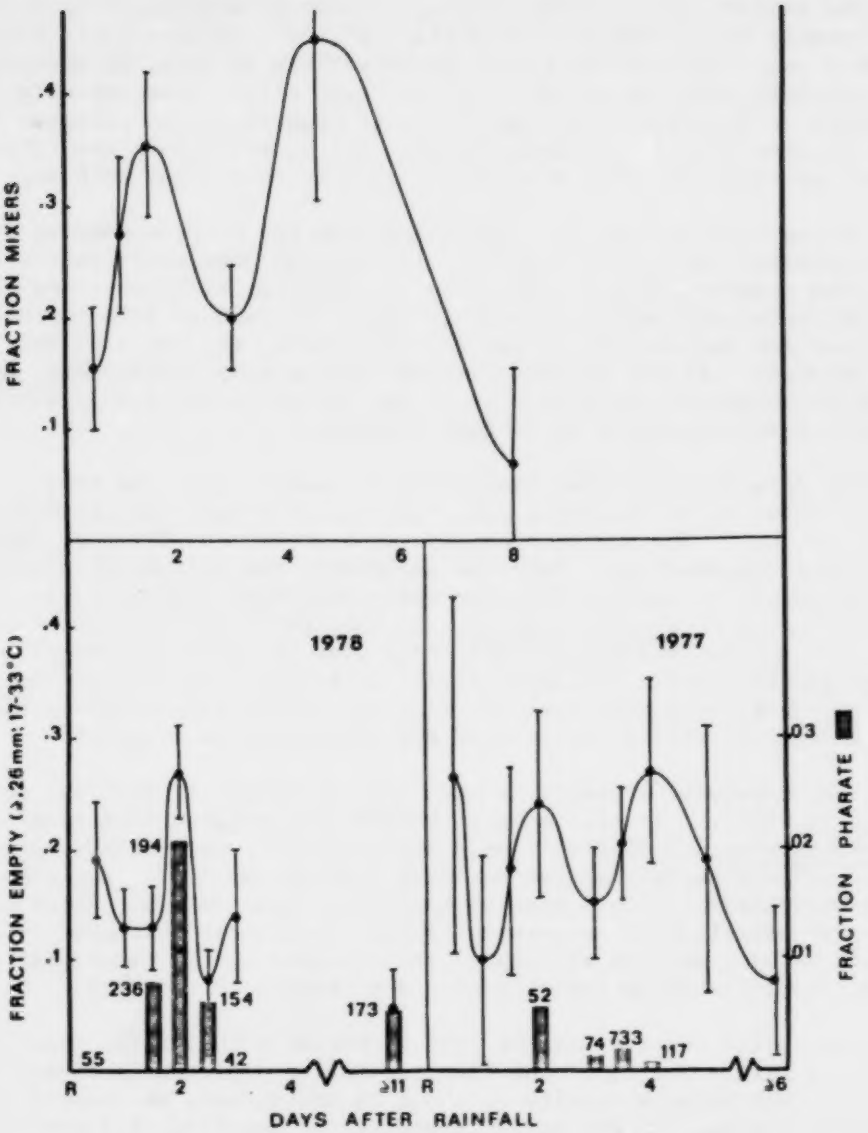


FIGURE 5. The relationship of the fraction of mixers, the fraction empty and the fraction pharate to the timing of rainfall (R). The vertical bars show plus or minus two standard errors of the mean. The fractions empty are for large animals from 20 warm collection dates in 1978 and 21 in 1977. The numbers give the sample sizes in which pharate animals were observed.

DISCUSSION

The failure of the lower surfaces to catch springtails is evidence that locally the grease has a repellant effect. Those animals trapped probably come from outside the range detectable by their chemoreceptors. This suggests that all jumped onto the traps either spontaneously or following stimulation. Consequently, the numbers caught estimate immigration from beyond a minimum distance and underestimate the total numbers entering the area which would include those that walk in.

The data on the general population from the suction samples also underestimates the actual density. The unknown correction factor should take into account factors that influence sampling efficiency and those that influence the number of animals present. Because both the measures of mixing and density err in the same direction, the ratio of the two is more accurate. As the suction samples include many individuals, neither the distribution of gut contents nor the distribution of body sizes will be altered substantially by further increase.

The data indicate that immigrants are adults near the time of ecdyses. As a consequence of its empty gut, the lighter weight immigrant might travel further. The new microhabitat will provide a different food supply and affect reproduction. Both the immigrants and residents have access to new sources of gametes with the advantages that genetic variation confers. Females of Sinella curviseta in laboratory culture cannot retain sperm through the molting process; they pick up sperm and oviposit early in certain intermolts (Waldorf,1971). If E. socia is similar and conditions are favorable, by moving near the time of ecdysis many female immigrants can immediately utilize sperm from new associates to oviposit.

Some euedaphic springtails have diurnal cycles of vertical movements (Leuthold, 1961). My preliminary observations suggest that these characterize Entomobrya socia. Individuals were not visible to an observor at 4 PM, but were visible when the habitat was next examined at 7 PM. The time of upward movement coincides with a peak of horizontal immigration. After moving upward some animals tend to move laterally. Horizontal movements occur in intervals between periods of temperature extremes and in times that avoid the low air humidity characteristic of mid-afternoon (2 to 4 PM).

Population density was the primary variable that influenced the number of mixers per day. The linear relation depicted in Figure 4B suggests that below a density of about 20 individuals per sample (49,000mm^2) no mixing occurs. In two years of population sampling this density or a lower density characterized from January through March of both years and July through December of 1977 (Waldorf, unpublished).

More data on mixing would allow an evaluation of the ecological relation of mixing to population density. How does the fraction of mixers vary with increasing population density?

By synchronizing molting, rainfall indirectly affects the timing of most mixing. It tends to synchronize immigration. The blooms of bacteria that follow rainfall possibly supplement the diet and accelerate the breakdown of other organic foods. As a consequence immigrants might be more likely to find an abundance of available food. CO_2 experimentally introduced stimulates increased horizontal movement in epigeic species (Joosse and Kapteijin,1968). Since a burst of CO_2 is generated by microbiol activity shortly after rainfall, natural CO_2 might stimulate the peak of mixing following rainfall.

SUMMARY

When individuals of E. socia that moved horizontally in their natural habitat were compared with individuals of the general population, the mixers were found to be of large body size and more likely to have empty guts. The numbers of mixers varied through the 24 hour cycle with maxima at 9 to 11 AM and 5 to 9 PM. The number per day was dependent primarily on population density. Two peaks of mixing occur in the days following rainfall; these coincide approximately with peaks of fasting and molting in the general population.

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THE EFFECTS OF TRAMPLING ON THE FAUNA OF A FOREST FLOOR.

I. MICROARTHROPODS

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France

INTRODUCTION

Periurban forests have an important social function as recreation areas . However, soil structure and life,especially, are sometimes seriously troubled by trampling effects. So, it is of importance to have ecological indicators able to give us information on the evolution of a disturbed edaphic ecosystems .

To appreciate pollution effects, investigations have been carried out not only on Lichens and Bryophytes (Gilbert ,1970), but also on Macrofauna (Novakova,1969; Gilbert,1971) ,and Microarthropods (Lebrun,1976; Bolle et.al.,1977) . On the other hand, a limited number of studies have been concerned with trampling effects in forests (Liddle,1975).

The aim of the present study is to analyse the relationship between Microarthropods and soil modifications under trampling influence . According to its role in soil dynamics and its high specific richness and density,studies of this fauna may give a more precise and complete information on the perturbation level,than any abiotic factor of the ecosystem .

Study area

The work was carried out in a section of the Fontainebleau Forest, near Paris, which is frequently visited by tourists . The area is located along a road,in front of a parking lot, and is used for picnics and recreation. Trees are beeches (*Fagus silvatica* L.), and oaks (*Quercus sessiliflora* Smith); near the road there are also a few pines (*Pinus silvestris* L.).

METHODS

Soil analysis

Three parameters were distinguished: humidity,organic matter and porosity. Sampling was made along five rows parallel to the road and 10 m. apart.Row n^{o}1 was at 5m from the road and under the pine trees. In each row five cilindrical sample units were taken (diameter 5 cm.). Where a holorganic horizon (H) existed,it was removed .

Each sample unit was immediately weighed and its heigth was measured; after drying at 85°C to constant weigth, humidity was calculated. The organic matter was measured by the Anne method on the fine particles (less than 2 mm.). Debris greater than 2mm in diameter was weighed in order to estimate the total amount of organic matter. Estimation of porosity was made according to Duchaufour (1960). As the soil lies on eolian sand, the real soil density was calculated from the sand density, corrected by taking into account the total organic matter concentration .

Microarthropods sampling

The Microarthropods sampling, realized on the 9th January 1978, was made along six rows parallel to the road and 10m. apart,except for the sixth row which was only 5m. away from the fifth. In each row, five sample units were taken (diameter 5cm.). The L and F layer as well as 5cm. of soil were separated .

Microarthropods were extracted in a high gradient extractor. After extraction, litter was dried at 85C to constant weigth. The soil was treated as before in order to mesure the organic matter concentration .

RESULTS

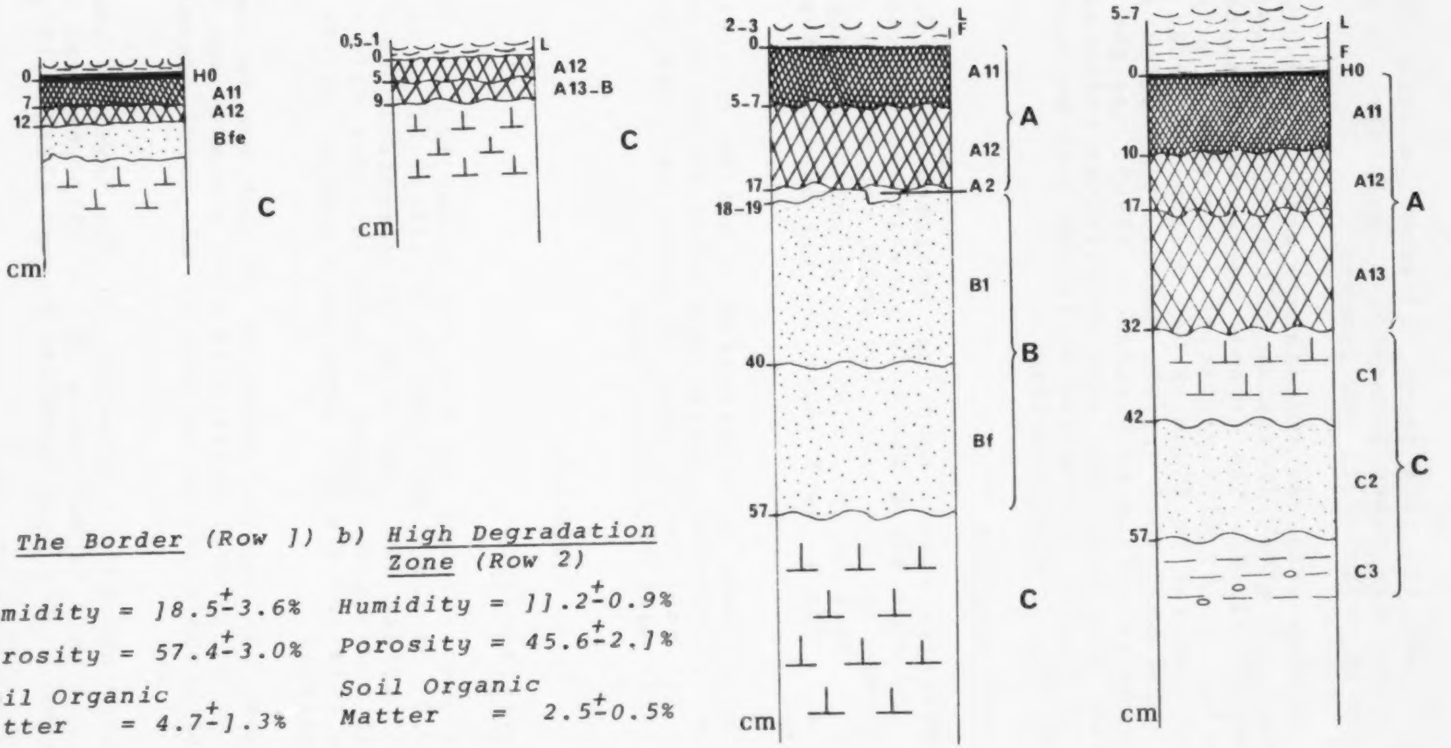
Station caracteristics

Results concerning the soil are summarized in figure 1, tables 1 and 2. As there are pines and patches of grass along the road, the border row (row 1) is not comparable to others: here the soil shows a mor humus (figure 1a). For this reason, results from this row are not taken into account in the correlation analysis .

The most distinctive parameter of each row is humidity (see table 1). It is well correlated with porosity and the amount of soil organic matter as well as the total organic matter (table 2) .

Porosity presents a threshold at the level of row four in which it reachs a normal value (53 to 65%) obtained for the same substratum in the Fontainebleau Forest (Faille,1977).

However,for those normal values of porosity the concentration of soil organic matter is significantly higher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A11
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A13
C1
C2
C3
A
C

a) The Border (Row 1)

Humidity = 18.5±3.6%

Porosity = 57.4±3.0%

Soil Organic
Matter = 4.7±1.3%

b) High Degradation Zone (Row 2)

Humidity = 11.2±0.9%

Porosity = 45.6±2.1%

Soil Organic
Matter = 2.5±0.5%

(Row 3)

Humidity = 15.7±1.7%

Porosity = 47.9±2.1%

Soil Organic
Matter = 2.9±0.8%

c) Transition Zone

(Row 4)

Humidity = 24.3±3.8%
Porosity = 57.6±2.4%
Soil Organic
Matter = 4.1±0.7%

d) Mosaic Zone (Accumulation spots)
(Row 5)
Humidity = 34.7±12.0%
Porosity = 58.2±4.2%
Soil Organic
Matter = 5.9±1.5%

FIGURE 1 . Soil profils - Humidity,porosity and level of organic matter.

in row 5 than in row 4 (figure 1c,d).Values for row 4 are lower than the usual ones for a moder humus in the Fontainebleau Forest : 4.7% (Robin,1971) .

TABLE 1 - Comparison of humidity,porosity and organic matter concentration between the rows (R) . Nonparametric U-test. ○:no significant; ★:significant; ★★:very significant.

	R_1R_2	R_1R_3	R_1R_4	R_1R_5	R_2R_3	R_2R_4	R_2R_5	R_3R_4	R_3R_5	R_4R_5
Humidity	★★	★★	★★	★★	★★	★★	★★	★★	★★	★★
Porosity	★★	★★	○	○	★	★★	★★	★★	★★	○
Soil Organic Matter	★★	★★	○	○	○	★★	★★	★★	★★	★★
Total Organic Matter					○	★★	★★	★★	★★	○

TABLE 2 - Correlations between humidity,porosity and organic matter . α = α-error . The estimates were made from the raw data . n = 20 .

	Soil Organic Matter (% of soil dry weigth)	*Total Organic Matter (% of soil dry weigth)*	*Porosity (%)*
Humidity (% of soil dry weigth)	$r = 0.94$ $b = 0.14$ $a = 0.87$ $\alpha = 10^{-8}$	$r = 0.96$ $b = 0.27$ $a = -0.26$ $\alpha = 10^{-8}$	$r = 0.82$ $b = 0.47$ $a = 42.19$ $\alpha = 10^{-4}$
Porosity (%)	$r = 0.83$ $b = 0.21$ $a = -7.26$ $\alpha = 10^{-5}$	$r = 0.85$ $b = 0.41$ $a = -13.82$ $\alpha = 10^{-5}$	

According to these observations,four different situations can be distinguished :

i) The border (row one); somewhat comparable to rows 4 and 5 for porosity and concentration of organic matter but with a different humus type (figure 1a).

ii) The high degradation zone (rows two and three) ; with a porosity lower than normal , a very low concentration

TABLE 3 - Estimates of the densities (ind/m^2) by rows and by group of Microarthropods .

The relative errors (er.) were estimated from : $S_e^2 = \frac{D^2}{NS}(\frac{1}{D} + \frac{S}{K})$ from Berthet et al.(1970); $D^2 = \frac{t^2S^2}{n\ \bar{x}^2}$ or $D^2 = \frac{t^2}{n\bar{x}}$ according to the relation between $\bar{x}$ and s^2 and the values of k (Elliot,1971) . High relative errors are due to the extremely low densities and to the proportion of zeros in the sample-units .

	Row 1	Row 2	Row 3	Row 4	Row 5	Row 6
Prostigmata	3,107 ± 626	560 ± 209	560 ± 209	3,107 ± 626	12,783 ± 4,774	12,783 ± 4,774
Acaridiae	6,987 ± 867	6,987 ± 867	6,213 ± 944	6,987 ± 867	25,668 ± 5,260	10,084 ± 2,914
Gamasida Uropoda	0	0	0	0	1,630 ± 552	1,630 ± 552
Gamasida Parasitodea + Zerconidae	713 ± 185	0	0	1,120 ± 712	6,264 ± 2,389	6,264 ± 2,389
Collembola Arthropleona	1,767 ± 759	1,767 ± 759	1,767 ± 759	11,204 ± 5,175	65,648 ± 20,085	65,648 ± 20,085
Collembola Symphypleona	9,167 ± 2,052	998 ± 218	1,731 ± 594	1,732 ± 594	306 ± 249	306 ± 249
Oribatida	775 ± 286	775 ± 286	775 ± 286	775 ± 286	24,995 ± 9,921	24,995 ± 9,921

of organic matter and a high reduction of water content . The absence of F layer indicates that the organic matter cycle is upset . In fact,leaves are swept out from this zone during winter and spring and accumulate at the level of row 5 according to the microtopography . The low values of organic matter concentration correspond with the profiles: the A_{11} horizon is missing in row 2 (figure 1b) and a A_{11} horizon of only 1-2 cm is observed at the level of row 3 . This zone presents a layer of 0.5-1 cm of very leached sand between litter and soil . Some further drillings demonstrated other abnormalities in the profiles,as superficial recasting of sand and leaching patches .

iii) The transition zone(row four),with a very thin F layer. The porosity is normal . The low concentration of organic matter and a discontinuity,represented by a shallow layer (0.5 cm) of leached sand between the F layer and the A_{11} horizon,suggest that the organic matter cycle is disturbed (figure 1d) .

iv) The mosaic zone (row five) . This is a patchy zone and we have chosen for sampling places where accumulation exists. The litter can reach a depth of 7 cm or more . The porosity is normal but the organic matter concentration is very high: 5.9 ± 1.5% (figure 1d) .

The microarthropod communities

Quantitative and qualitative characterization

Results are summarized in table 3 and figure 2 . A comparative analysis of the different rows shows that the microarthropod groups appears or increase in density in passing from the high degradation zone (row 2 and 3) to the mosaic zone (row 5 and 6) . However Collembola Symphypleona have a different pattern . In effect,their abundance decreases towards the mosaic zone in which they are almost absent . In addition,this group is significantly more abundant in the border row (U-test,$\alpha=0.028$)

The Acaridiae,98% of which belong to the Tyroglyphidae, present the maximal density in row 5 (U-test,$\alpha=0.028$) .

The density and presence or absence of the different groups allow to distinguish four Microarthropod communities. These correspond to the soil zones described before (figure 2).

i) The border community (row one) is characterized by the Symphypleona and the Acaridiae (41% and 31% of the total

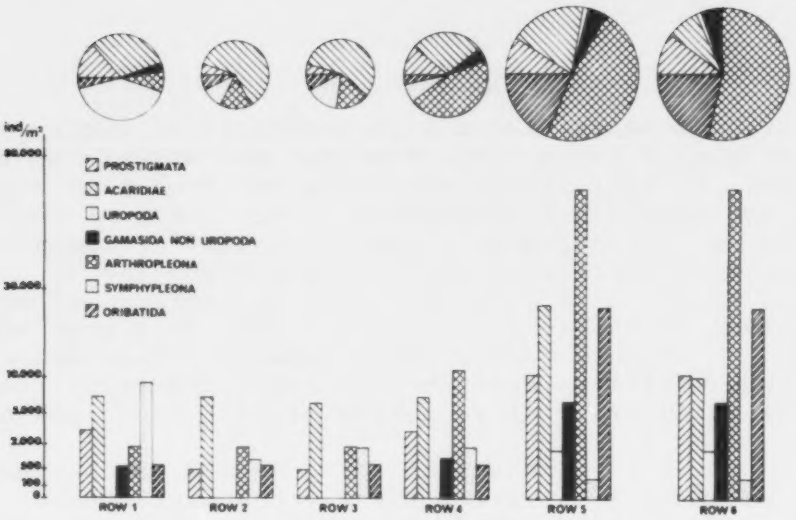

FIGURE 2 . Densities (histograms) and relative abundances (circles) of Microarthropods in the different rows of samples . Circle surfaces are proportional to the square root of the total density in each row .

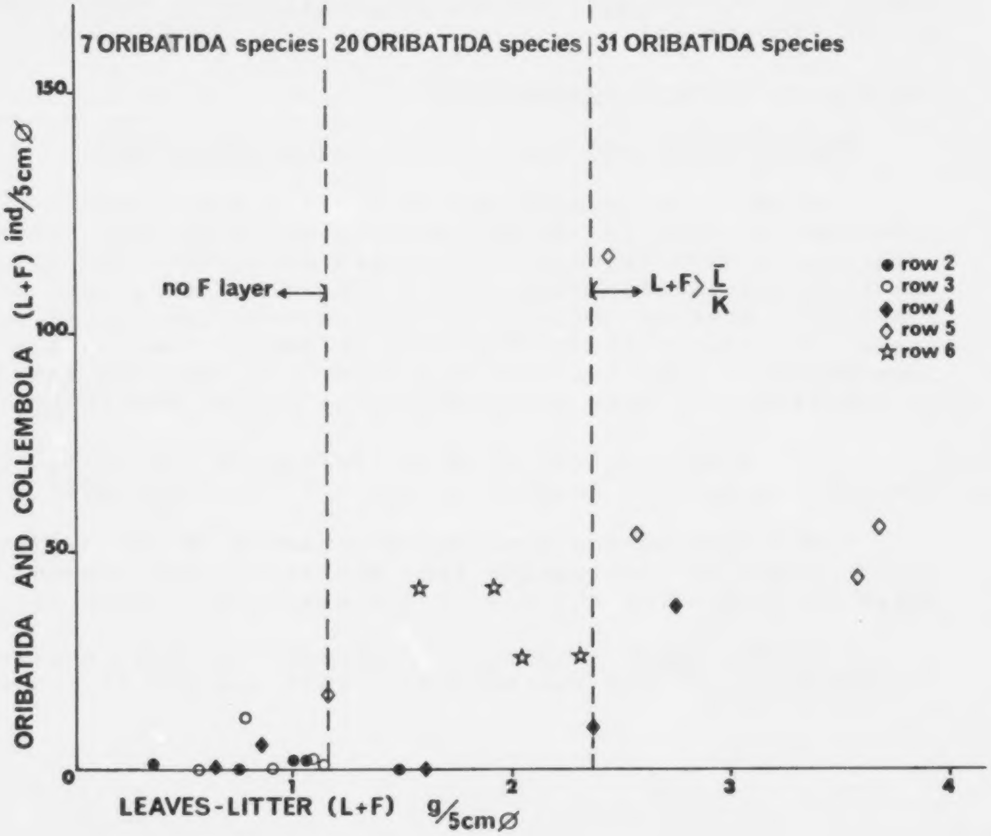

FIGURE 3 . Relation between the numbers of Collembola-Oribatida (L+F) and the dry weigth of extraction leaves litter .

density respectively) and by the absence of the Gamasida Uropoda . Oribatida and Arthropleona are present, but in very low numbers .

ii) The high degradation zone community (rows two and three) . In this zone, the total density of Microarthropods is ten times less than in the mosaic zone . The community can be characterized by the dominance of Acaridiae (63% of the total density) , by the absence of Gamasida (both: Uropoda and non-Uropoda) and by the very low density of Oribatida: 775 ± 286 ind./m^2 .

iii) The transition zone community (row four) . In this zone the Microarthropod density is twice that of the previous zones . Arthropleona are dominant (45% of the total density), while the relative abundance of Acaridiae decreases (28%) ; this is also the case for Oribatida and Symphypleona . Gamasida non-Uropoda are present .

iv) The mosaic zone community (rows five and six) . The only significant difference between the two last rows concerns Acaridiae densities (U-test, $\alpha=0.005$) . The other Microarthropods have similar densities in the two rows . Arthropleona represents 47.8% of the total density in row 5 and 54% in row 6 . The density of Oribatida is about 32 times higher than in other zones and their relative abundance is 18% and 20.5% in rows 5 and 6 respectively . Gamasida Uropoda are present .

Relationships between Microarthropods, litter and soil organic matter

Table 4 shows that the total number of Microarthropods in each core sample is significantly correlated with the litter (L + F), dry weigth and also with the organic matter concentration in the soil . This is not surprinsing, inasmuch as the organic matter and the litter are not independent ($r=0.43$; $\alpha=0.01$).

However, the correlation between litter Microarthropod's number and the amount of litter is significantly higher than the correlation between the soil Microarthropod's number and the organic matter : $r_1 > r_4$; $\alpha=10^{-6}$ (see table 4) . This is also true for Collembola and Oribatida alone .

In a protected forest area the soil Microarthropods are independent of the soil organic matter (Garay,unpublished data). This is also observed,in a very different ecosystem,by Santos, De Pree and Whitford (1978), but they found a dependence between Microarthropods and the amount of litter . So, other parameters, different from the organic matter concentration,remain to be found in order to explain the distribution of soil Microarthropods .

TABLE 4 - Correlations between Microarthropods and the amount of litter, and between Microarthropods and the concentration of organic matter, in the core-samples. α= α-error .

	Microarthropods by level : (L+F) or soil	*Microarthropods by core-sample (L+F) and soil*	*Oribatida - Collembola by level (L+F) or soil*
Litter : L+F (g) *n = 25*	$r_1 = 0.84$ $b = 0.57$ $a = 49.48$ $\alpha = 10^{-6}$	$r_2 = 0.55$ $b = 72.42$ $a = -12.59$ $\alpha = 10^{-2}$	$r_3 = 0.86$ $b = 41.88$ $a = 41.51$ $\alpha = 10^{-7}$
Soil Organic Matter (%) *n = 24*	$r_4 = 0.37$ $b = 23.94$ $a = 39.17$ $\alpha = 0.08$	$r_5 = 0.54$ $b = 71.32$ $a = -11.00$ $\alpha = 0.01$	$r_6 = 0.41$ $b = 21.75$ $a = 47.71$ $\alpha = 0.05$

Nevertheless, in our disturbed area, a more detailed observation of data shows a threshold phenomenon in the transition zone: when the organic matter concentration is less than 4.8% , the number of Microarthropods is low and only for higher values of organic matter concentration the presence of aggregates may be observed .

Litter Accumulation and Microarthropods

In figure 3,representing the relationship between litter dry weigth per core-sample and number of litter Collembola and Oribatida,two dotted lines parallel to the Y-axis diferenciate three sets of points.The first line corresponds to the maximum amount of litter when there is not F layer (1.496g) and the second one corresponds to the value $X = \overline{L+F}$.

$\overline{L+F}$ was estimated from the value of the Jenny coefficient K,given by Lemee and Bichaud (1973) for an undisturbed area with the same substratum and the same vegetation :

$$K = \frac{L}{L + F} = 0.38$$

and

$$\overline{L} = \frac{\Sigma L_i}{25} = 0.905g$$

where L_i is the amount of L layer in the core-sample number i.

Thus, $\overline{L+F} = 2.38g$

Most of the points corresponding to the high degradation zone (rows 2 and 3) are included in the first set of points, while most of the points of row 6 and 5 are respectively included in the second and third set of points . The transposition between points of row 5 and 6 is due to the fact that litter coming from the high degradation zone accumulates in the normal region near the trampling area (row 5) . However, a point of high accumulation exists in row 6 due to microtopographic conditions: the amount of litter is 6.4 g and there are 407 Collembola and Oribatida .

The above results demonstrate that the number of Microarthropods is correlated with the amount of litter . Considering only the Oribatida, their core-sample number (litter and soil) is also significantly correlated with the corresponding litter quantity: $r=0.71$ ($\alpha= 10^{-7}$) . It is therefore of interest to study the specific composition of this group in order to compare the different categories of samples characterized in figure 3.

In the samples taken from the high degradation zone and represented between the Y axis and the line $x = 1.496g$, 7 species have been found in very low density : *Carabodes labyrinthicus* (Michael), *Camisia horrida* (Hermann), *Tectocepheus sarekensis* Tragardh, *Phthiracarus nitens* (Nicolet), *Achipteria coleoptrata* (L.), *Chamobates pusillus* (Ber) and *Chamobates incisus* .

In the samples represented between $x = 1.496g$ and $x = 2.38g$, 20 species have been found . The Oppidae are represented by *Oppiella insculpta* (Paoli), *Oppiella minus* (Paoli) . The Brachychthoniidae by *Brachychthonius impressus* Moritz, *Liochthonius simplex* (Forsslund) and *Liochthonius cf. tuxeni* (Forsslund). The Suctobelbidae by *Suctobelbella sarekensis* (Forsslund), *Suctobelbella cf. perforata* (Strenzke) and *Suctobelbella subcornigera* (Forsslund) .

In the samples corresponding to litter accumulation, 31 species were identified . Among them there are 3 species of Oppidae: *O. insculpta, O. minus, Oppiella nova* (Oudemans); 9 species of Brachychthoniidae: *B. impressus, Brachychthonius bimaculatus* Willmann, *Brachychochthonius suecicus* Forsslund, *Brachychochthonius cf. jacoti* (Evans), *Brachychochthonius rostratus* (Jacot), *L. tuxeni, Liochthonius horridus* (Sellnick), *Liochthonius brevis* (Michael), *Paraliochthonius piluliferus* Forsslund; and 5 species of Suctobelbidae: *S. cf. sarekensis, S. cf. perforata, S. subcornigera, Suctobelbella intermedia* (Willmann), *Suctobelbella nasalis* (Forsslund) .

The accumulation places are characterized by an important increase of specific richness, which is mostly due to species generally considered as microphytophagous . This fact suggests that the trophic conditions can be modified by litter accumulation .

CONCLUSIONS

A comparative analysis of Microarthropod patterns in the study area allows us to classify them according to their reaction to perturbations induced by trampling .

Three groups may be distinguished : i) The first group includes species which seems to be opportunist . This is the case of Acaridiae Tyroglyphidae, a family comprising species living in different environments as stored foods,human and animal habitats, agricultural soils treated with pesticides (Karg,1979) . Some Prostigmata are equally found in the high degradated zone and are thus capable of living in extreme conditions, but usually in small numbers .

ii) A second group includes species belonging to Symphypleona and Oribatida adapted to open spaces where the microclimate shows important variations: some Symphypleona are known for their ability to live in open environments thanks to various morphological and physiological adaptations (Betsch,Betsch and Vannier, 1979) . This is also true for Oribatida like *Camisia horrida* , *Carabodes labyrinthicus* and *Tectocepheus sarekensis* which we have not only found in the degradated zone of the study area but also in the parking lot . These species are known for their ability to live in environments showing extremely variable conditions .

iii) The third group consists of species whose absence or low densities in the disturbed zones express various sensibilities to trampling : a) a first set includes very sensitive species which only exist where porosity,soil organic matter and litter structure are normal . These species belong to Uropoda and the Oribatida: Oppidae, Suctobelbidae and Brachichthoniidae which are mainly microphytophagous living in humus layer . b) another set is formed by less sensitive species capable of surviving in an environment partially modified by trampling . This is the case of Arthropleona and Gamasida non-Uropoda . The number of these predators is normally correlated with that of Collembola which are their potential preys (Blandin et.al.,in press) .

These observations allow us to propose the use of Microarthropods as indicators of trampling damage . In particular,this could be of practical usefulness for the evaluation of the threshold beyond which these damages are irreversible.

Taking into account the overall quantitative and qualitative changes undergone by the community of Microarthropods,precise indications could be obtained . The quantitative variations of a single species - or category- do not allow to draw definitive conclusions, although these could be provided by the comparative study of species having different sensibilities . It is therefore the whole community which could be a good ecological indicator of the trampling impact .

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THE EFFECTS OF TRAMPLING ON THE FAUNA OF A FOREST FLOOR.

II. MACROARTHROPODS

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INTRODUCTION

Based on the observation obvious to any biologist, that environmental conditions quite clearly determine the living beings present, one may conversely seek to describe the physical environment through the organisms that inhabit it. In fact, ecologists constantly employ different organisms as indicators, in order to characterize certain situations or phenomena which are difficult to approach directly.

In aquatic environments, the use of estimates of quantitative and qualitative changes in animal communities as bioindicators in the examination of certain alteration factors (water pollution) is highly applied. On the contrary in the case of terrestrial environments these methods are still in the research stage (Novacova, 1969 ; Gilbert, 1971 ; Liddle, 1975 ; Lebrun, 1976).

The position of animals in the trophic sequence of ecosystems accounts for an ability of integration greater than that of vegetation. This should motivate research of ecological indicators in order to detect, define, and measure the levels of global perturbation in ecosystems.

Since January 1978 we have been engaged in a research project on the Macroarthropods community as indicator of evolutionary tendencies in suburban woodland areas. This work seeks to define multispecific groups, able to provide precise indications on the state and evolution of suburban forestrial environments. In particular we concentrate our interest on the effects of trampling on the Macroarthropods of the woodlands floor which are subject to a high frequentation rate.

Study area

The forest of Fontainebleau, situated 60 km away from Paris, was chosen for our investigations, as it supports particularly heavy visitation rates. The forest attracts 9,000,000 visitors per year i.e. an average of 25,000 visitors per day (S.A.R.E.S., data for 1969). For sampling area, it was chosen a 0.2 ha woodland section. The average altitude is 100 m. The regions mean annual temperature is 10.1°C and the mean annual rainfall 697 mm. Some characteristics of temperatures and rainfalls annual repartition are presented in figure 1. The section's canopy consists of *Fagus silvatica* L. with some *Quercus sessiliflora* Smith, lofty trees. Six *Pinus silvestris* L. are along bordering road. There is no ground vegetation.

FIGURE 1. Average monthly temperatures in °C and rainfall in mm in the Fontainebleau region (data from Météorologie Nationale).

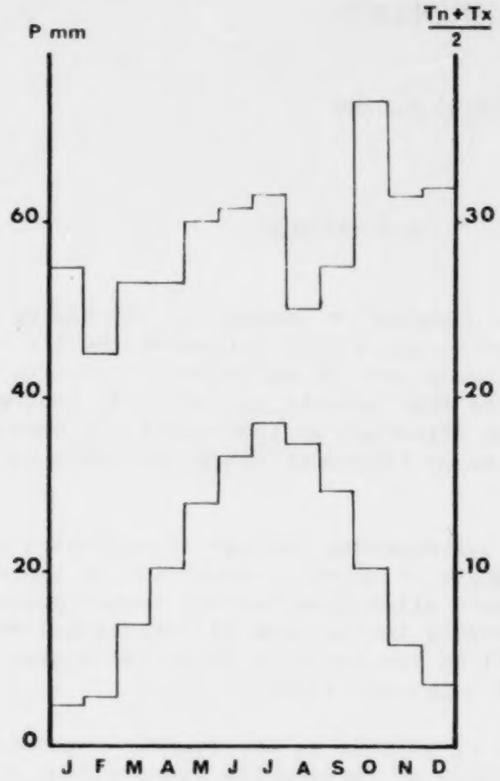
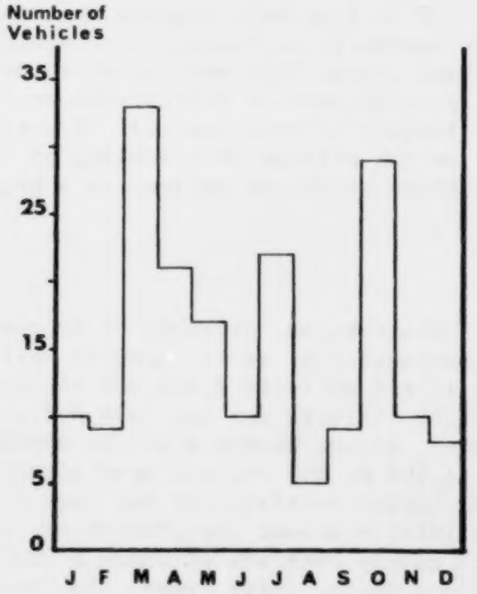


FIGURE 2. Average monthly visitation rates in the parking lot in of the study area (data from the observation of the number of vehicles during week ends.



An important reason for the choice of this area was that a parking lot is situated in front of this section, from the other side of the road. So the frequentation rates were expected to be higher than the average values of Fontainebleau as it is known that most visitors frequent particular areas which offer certain conveniences (parking lots, easy access). People also, do not leave their vehicles more than 100 m behind, thereby remaining within very limited areas (Baillon, 1973). Researches in forestrial environments on the influence of trampling in vegetation, have pointed out that in such zones the tourist impact and the degradation of soil and vegetation are considerable (Fallinski, 1973 ; Littel, 1974).

Annuals litter evolution

Litter's evolution was followed by pictures every week from January 1978 to January 1979. In the end of November the floor is covered from the leaves fallen during Autumn. Progressively under the wind's influence and as the soil is subsided, leaves accumulate more or less in certain places according to the microtopography. So during January and February, only in the background of the section we can observe an undisturbed litter which shows three distinct layers :

i) The L layer formed by leaves which fell during the previous Autumn.
ii) The F layer which consists of partly decomposed leaves.
iii) The H layer which consists of amorphous humus.

In Spring, three zones parallel to the road can be recognised:

i) The first is almost nude, but however with small spots of accumulated litter. It will be called from now on zone of high degradation.

ii) The transition zone corresponds in the area where litter accumulates in wide spots, but some places remain nude.

iii) The last zone seems to be relatively undisturbed showing an abundant and permanent litter.

Frequentation of the study area

All throughout 1978, the number of vehicles in the parking lot area, was observed and frequentation rates of the section were estimated. The histogram traced from these data, points out the bimodality of frequentation with two maxima, during March-April and October (figure 2), a finding that corresponds to the general frequentation of the forest of Fontainebleau.

METHODS

After a preliminary sampling in June 1978, it was decided to do series of samples every three months, starting from November 1978. The preliminary sampling pointed out the existence of a certain gradient in the spatial distribution of Macroarthropods. Thus, we decided to collect samples along four rows parallel to the road and fifteen meters apart. Seven sample units were taken in each Row. Samples were limited by a 25 x 25 cm metal frame inside which litter was collected. Samples in February and May, for the first two Rows, were collected in spots where litter was accumulated and not in the completly nude soil. Litter was kept in paper bags, and back in the laboratory was put in Berlese-Tullgren funnels with light as heat source for fifteen days, adequate duration for the extraction of all the Macroarthropods (Geoffroy, 1979). Animals were collected in recipients containing Salycilic Acid.

RESULTS

Results are summarized in tables 1, 2, 3 and figures 3, 4, 5, 6, 7, 8, 9, 10. A complete absence of certain groups of Macroarthropods such as Isopods, Pseudoscorpions and Opilions, everywhere in the area, is observed. An extremely low presence of other groups such as Diptera, Diptera larvae, Coleoptera, Coleoptera larvae and Millipedes are observed to exhibit important densities, unless in certain periods and usually in the background of the section (figures 5, 6, 7, 8, 9). On the other hand, the Spiders and Centipedes are present, but in low densities and not throughout the whole sampling period (figures 3, 4).

TABLE 1. Estimates of the densities (ind./m^2) by Rows and by groups of Macroarthropods in November sampling. The relative errors (er) were estimated from $r_e = \frac{D^2}{NS}\left(\frac{1}{2} + \frac{S}{K}\right)$, Berthet and Gérard, 1970 ; $D^2 = \frac{t^2S^2}{n\bar{x}^2}$ or $D^2 = \frac{t^2}{n\bar{x}}$ according to the relations between $\bar{x}$ and S^2 and the values of K (Elliot, 1971). Great relative errors are due to the extremely low densities. * one individual per Row ; * *two individuals per Row.

	ROW 1	ROW 2	ROW 3	ROW 4
Spiders	10.3 ± 6.2 er : 60 %	10.3 ± 6.2 er : 60 %	22.9 ± 19.0 er : 83 %	48.0 ± 16.0 er : 33 %
Centipeds	3.4 ± 2.7 er : 79 %	3.4 ± 2.7 er : 79 %	11.4 ± 9.9 er : 86 %	12.2 ± 7.5 er : 61 %
Millipedes	0	12.2 ± 7.5 er : 61 %	12.2 ± 7.5 er : 61 %	12.2 ± 7.5 er : 61 %
Diptera	20.0 ± 8.2 er : 41 %	20.0 ± 8.2 er : 41 %	20.0 ± 8.2 er : 41 %	20.0 ± 8.2 er : 41 %
Coleoptera	65.1 ± 15.8 er : 24 %	65.1 ± 15.8 er : 24 %	125.7 ± 30.5 er : 24 %	125.7 ± 30.5 er : 24 %
Dipt. Larvae	377.1 ± 274.3 er : 73 %	379.0 ± 84.0 er : 22 %	379.0 ± 84.0 er : 22 %	379.0 ± 84.0 er : 22 %
Col. Larvae	97.6 ± 15.5 er : 16 %	97.6 ± 15.5 er : 16 %	97.6 ± 15.5 er : 16 %	97.6 ± 15.5 er : 16 %
Ants	0	* *	4.1 ± 2.4 er : 59 %	4.1 ± 2.4 er : 59 %

AVERAGE DENSITY (ind./m^2) IN NOVEMBER (black rectangle), FEBRUARY (solid rectangle) AND MAY (empty rectangle) FOR THE FOUR PARALLEL ROWS.

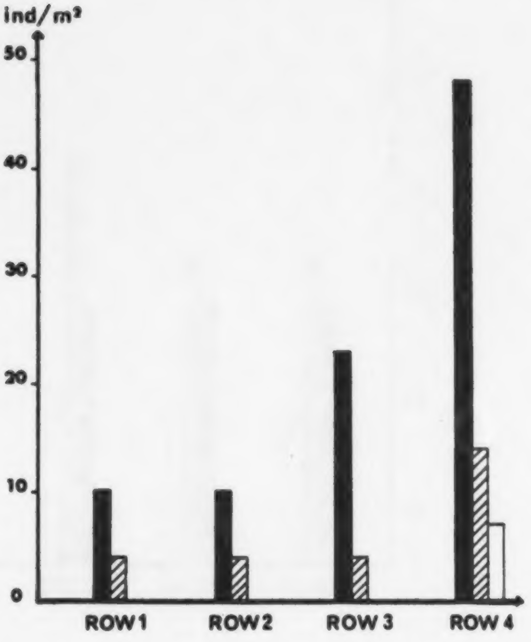


FIGURE 3. **SPIDERS**

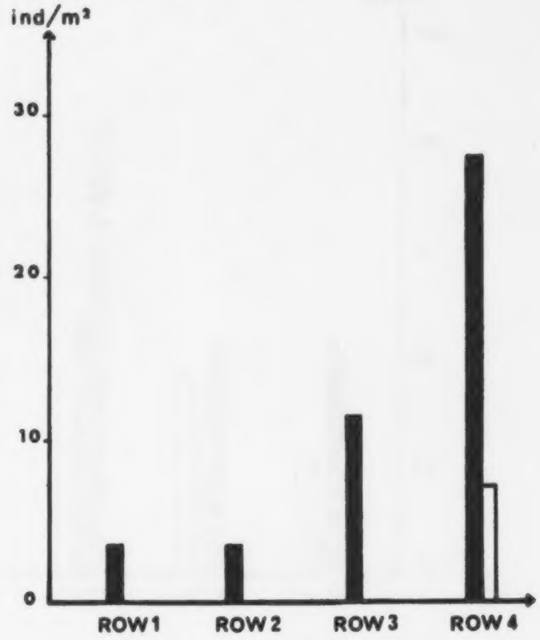


FIGURE 4. **CENTIPEDES**

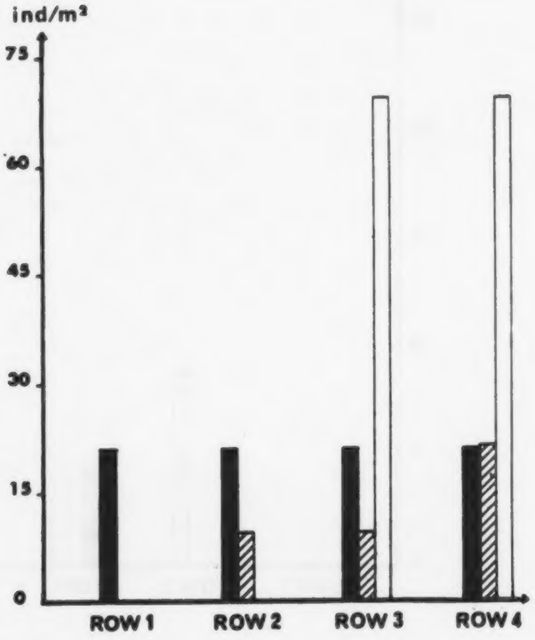


FIGURE 5. **DIPTERA**

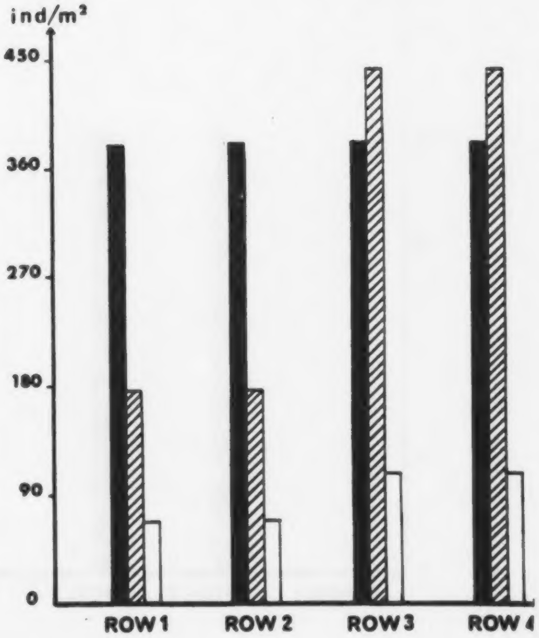


FIGURE 6. **DIPTERA LARVAE**

AVERAGE DENSITY (ind./m^2) IN NOVEMBER (black rectangle), FEBRUARY (solid rectangle) AND MAY (empty rectangle) FOR THE FOUR PARALLEL ROWS.

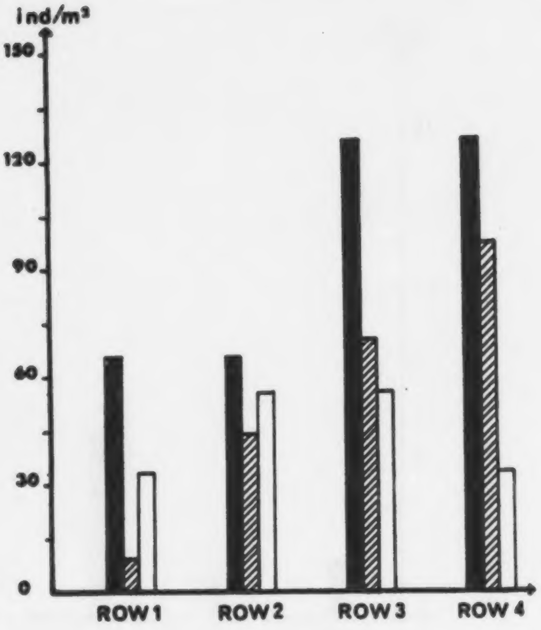


FIGURE 7. **COLEOPTERA**

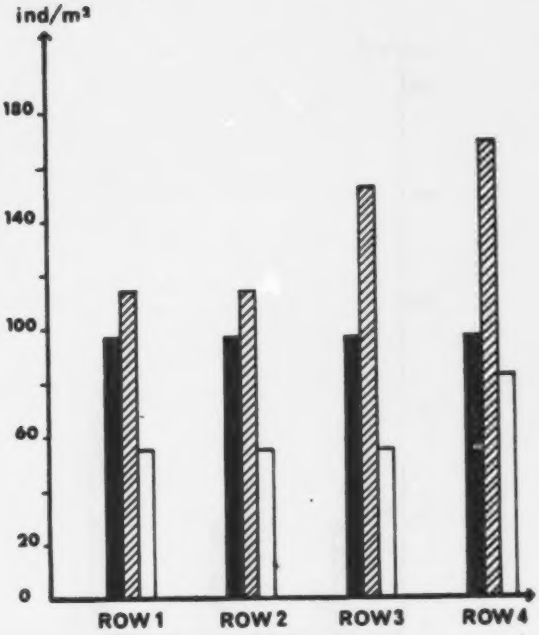


FIGURE 8. **COLEOPTERA LARVAE**

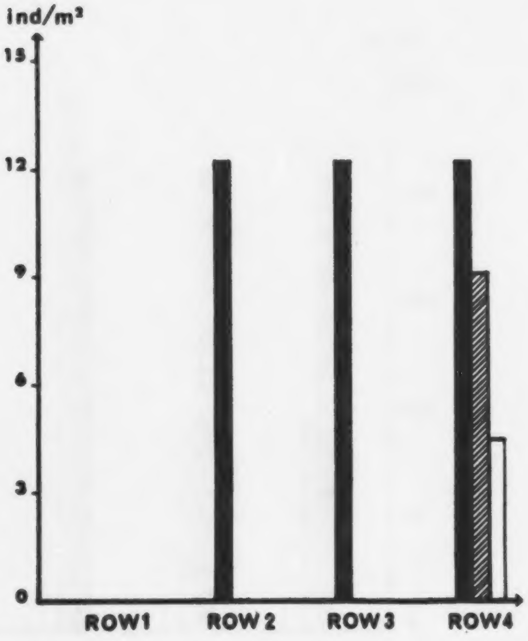


FIGURE 9. **MILLIPEDES**

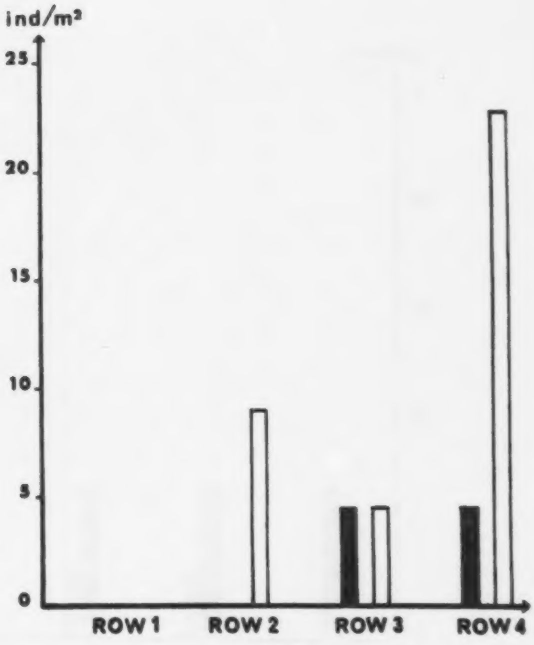


FIGURE 10. **ANTS**

TABLE 2. Estimates of the densities (ind./m^2) by Rows and by groups of Macroarthropods in February sampling.

★ one individual per Row (Seven sample units) ;
★ ★two individuals per Row (Seven sample units).

	ROW 1	ROW 2	ROW 3	ROW 4
Spiders	3.8 ± 2.2 er : 57 %	3.8 ± 2.2 er : 57 %	3.8 ± 2.2 er : 57 %	13.7 ± 12.0 er : 87 %
Centipeds	★ ★	0	0	6.9 ± 3.9 er : 56 %
Millipedes	0	0	★	9.1 ± 7.4 er : 81 %
Diptera	0	10.2 ± 7.1 er : 69 %	10.2 ± 7.1 er : 69 %	20.5 ± 15.1 er : 73 %
Coleoptera	9.1 ± 7.0 er : 76 %	43.4 ± 27.6 er : 63 %	70.0 ± 23.6 er : 33 %	96.0 ± 42.4 er : 44 %
Dipt. Larvae	169.0 ± 45.8 er : 27 %	169.0 ± 45.8 er : 27 %	433.0 ± 140.0 er : 32 %	433.0 ± 140.0 er : 32 %
Col. Larvae	114.2 ± 29.9 er : 26 %	114.2 ± 29.9 er : 26 %	153.0 ± 38.3 er : 25 %	169.1 ± 62.3 er : 36 %
Ants	0	0	0	0

TABLE 3. Estimates of the densities (indi/m^2) by Rows and by groups of Macroarthropods in May sampling.

★ one individual per Row (Seven sample units) ;
★ ★two individuals per Row (Seven sample units).

	ROW 1	ROW 2	ROW 3	ROW 4
Spiders	0	0	0	6.8 ± 5.9 er : 86 %
Centipeds	0	0	0	0
Millipedes	0	0	★	★ ★
Diptera	★ ★	0	70.7 ± 10.9 er : 15 %	70.7 ± 10.9 er : 15 %
Coleoptera	33.1 ± 8.8 er : 26 %	56.0 ± 21.4 er : 38 %	56.0 ± 21.4 er : 38 %	33.1 ± 8.7 er : 26 %
Dipt. Larvae	64.0 ± 25.1 er : 39 %	64.0 ± 25.1 er : 39 %	112.0 ± 29.6 er : 26 %	112.0 ± 29.6 er : 26 %
Col. Larvae	55.5 ± 18.8 er : 33 %	55.5 ± 18.8 er : 33 %	55.5 ± 18.8 er : 33 %	82.2 ± 13.2 er : 16 %
Ants	0	8.5 ± 3.5 er : 41 %	4.1 ± 2.4 er : 58 %	23.0 ± 15.8 er : 68 %

Quantitative and qualitative characteristics

Results of non parametric U-test comparizon between different groups and Rows in the three periods of sampling, are summarized in table 4. The values of U-test comparizon of all the groups densities between Rows one and four are highly significant. All the groups show much higher average densities in Row four than in Row one. Millipedes and Ants are not even present in Row one in any sampling period. Only in the case of Diptera, Diptera Larvae and Coleoptera Larvae in November sampling were the densities practically the same, between these two Rows (figures 5, 6, 8).

In the intermediate area between Rows one and four, the differences in the group average densities, seem to be not so clear. No difference in the densities between Row two and Row three for almost all the groups, could be observed (Millipedes, Spiders, Diptera, Diptera Larvae and Coleoptera Larvae in November sampling, Diptera in February and Coleoptera adults and Larvae in May sampling). Some groups, also, have densities not significantly different, between Rows one and two (Coleoptera in November's sampling, Diptera Larvae and Spiders in May's sampling), as well as between Rows three and four (Coleoptera in November, Diptera Larvae in February, Diptera adults and Larvae in May).

Thus, we see that the main distinction existing between the Macroarthropod densities is this between Rows one and four. In the intermediate Rows the groups-except from the predators- have similar densities.

The Macroarthropod communities

Taking into account the groups present and absent in each Row, and their relative abundances, three Macroarthropod communities could be distinguished, corresponding more or less directly to the intensity of perturbation.

In the first zone, corresponding to Row one, the community is characterized by the complete absence of Millipedes and Ants (figures 9, 10), by the partial absence of Spiders, Centipedes and Diptera, and by a very important reduction of all the Macroarthropod densities. The dominant group is the Diptera Larvae.

The second zone (Rows two and three), is situated at an intermediate distance from the road. The community here is characterized by the appearence of the groups not existing in the previous zone. Nevertheless the densities of the Macroarthropod community in this zone are relatively low, lower than those in Row four. The groups of predators still existing in the section, seem to be most affected, showing the lowest relative abundance. Diptera and Coleoptera Larvae are still the dominant groups.

The third Macroarthropod community corresponds to the last sampling zone (Row four). Litter here is abundant with a vertical structure during winter corresponding to the three layers previously described. The perturbation of this zone by trampling seems to be negligible. Densities of certain groups such as Spiders and Centipedes are five and nine times respectively higher that those in the first zone.

TABLE 4. Non parametric U-test comparizon between Rows and different groups for all the sampling periods. Level of significance : 0.05.

● non significant ; ★ significant ; ★ ★ highly significant.

	NOVEMBER						FEBRUARY						MAY					
	R_1R_2	R_1R_3	R_1R_4	R_2R_3	R_2R_4	R_3R_4	R_1R_2	R_1R_3	R_1R_4	R_2R_3	R_2R_4	R_3R_4	R_1R_2	R_1R_3	R_1R_4	R_2R_3	R_2R_4	R_3R_4
Spiders	●	★ ★	★ ★	★ ★	★ ★	★ ★	●	●	★ ★	●	★ ★	★ ★	●	●	★ ★	●	★ ★	★ ★
Centipedes	●	★ ★	★ ★	★ ★	★ ★	★ ★	●	●	★ ★	●	★ ★	★ ★	●	●	●	●	●	●
Millipedes	★ ★	★ ★	★ ★	●	●	●	●	●	★ ★	●	★ ★	●	●	●	●	●	●	●
Diptera	●	●	●	●	●	●	★ ★	★ ★	★ ★	●	★ ★	★ ★	●	★ ★	★ ★	★ ★	★ ★	●
Diptera Larvae	★	★ ★	●	●	●	●	●	★ ★	★ ★	★ ★	★ ★	●	●	★ ★	○	★	★ ★	●
Coleoptera	●	★ ★	★ ★	★ ★	●	●	★ ★	★ ★	★ ★	●	★ ★	★ ★	★ ★	★ ★	●	●	★ ★	●
Coleoptera Larvae	●	●	●	●	●	●	●	★ ★	★ ★	★ ★	★ ★	●	●	●	★	●	★ ★	★ ★
Ants	●	★ ★	★ ★	★ ★	★ ★	●	●	●	●	●	●	●	★ ★	★	★ ★	★	★ ★	★ ★

A preliminar comparizon between the densities of Macroarthropods in this zone and those of a non trampled, similar forest floor was made. (Station Biologique de Foljuif, E.N.S., situated 20 km south of our study area, unpublished data). This comparizon points out that almost all the groups from the third zone of our study area have lower densities than those of the practicly non trampled floor. Nevertheless, Coleoptera have in all the sampling periods much higher densities than those of Foljuif.

However the composition of Macroarthropod community in this third zone appears not to differ significantly from this of the non perturbated floor.

Seasonal variations of the Macroarthropod communities

In the end of November litter is formed over the study area as an homogenous layer of leaves. This litter is rapidly inhabited by many groups (Table 1). Although litter is homogenously distributed, a certain gradient between Rows can be easily observed, for Spiders, Centipedes, Ants and Coleoptera. Other groups such as Diptera adults and larvae, Coleoptera Larvae, and even Millipedes seem to be unaffected in this period. During winter, with the litter's accumulation in the less trampled on places, the influence of perturbation is clearest in all the groups, which show progressively increasing densities from Row one to Row four. During Spring the intensity of trampling reaches its maximum (figure 2). The composition of the Macroarthropod community in Zones one and two is completely different from February to May sampling (Tables 2 and 3). Thus, Spiders, Millipedes, Ants and Diptera are completely absent from Row one and two while they show low densities in Rows three and four. Centipedes are absent from all the area.

The predator populations

The previous discussion focused on the spatial and temporal variations of the structure of Macroarthropods community under the influence of perturbations induced by trampling. We observed that the predators are affected the most, their densities responding almost directly to the intensity of perturbation factors. Spiders and Centipedes are practically the only predators remaining in the area. The density of Spiders increases progressivly from Row one to Row four. The number of species present, also follows this pattern : in November's sampling, we found only one species : *Leptyphantes flavipes* in Row one, two species, *Tiso vagans* (Bl.), *Theridium vittatum* C.L. Koch in Row two, and five species, *Centromerita concinna*,(Th.), *Leptyphantes minutas*, Bl., *Tiso vagans*, *Leptiphantes flavipes* Bl., *Centromenus aequalis* C.L. Koch, in Rows three and four.

The study of Centipedes shows that the Lithobiomorph do not appear all over the study area. Only one species of Geophilomorph *Schendyla nemorensis* C.L. Koch, was found in the first and the second zone, while four different species (three immatures and a *Brochygeophilies tryncorum* Meinert, were found in the third zone (Row four).

These results show the important relation which may exist between certain perturbation factors and the specific richness of the predator communities in the soil ecosystem.

CONCLUSIONS

The study of the Macroarthropod communities of a trampled on forest soil, focuse on certain aspects of their structure. First of all we wish to underline the complete absence of certain functional groups such as Pseudoscorpions and Opilions, whose the role as predators is important for the community. Also, the absence of the especially important for litter's decomposition group of Isopoda, is remarquable. The reasons of disappearence of these functionally and taxonomically very different groups, have to be identified. However, other predator groups such as Spiders, Centipedes and Ants are present in much lower densities than in non trampled on zones. The sampling by Rows, pointed out that their numbers and specific richness increase when the perturbation in the floor is less important (figures 3 and 4). Studies in ecosystems of different structures, also show that the predators are always affected the most (Novacova, 1969 ; Littel, 1974 ; Van der Ploeg and von Wijngaarden, 1975).

From the other hand, groups such as Diptera and Coleoptera seem to be no affected directly, showing however certain gradients in their densities corresponding to the intensity of perturbation.

Thus, Macroarthropods, which do not show the same preferences in habitat and nutrition, do not react in the same way, in trampling. Through the study of these reactions and the Macroarthropod communities modifications, it will be possible to measure the effects and to characterize the impact of perturbation induced by trampling.

ACKNOWLEDGEMENTS

This research was supported by the Ministère de l'Environnement et du Cadre de Vie under Grant n°77136. Mr Christophe T. and Geoffroy J.-J. for the Spiders and Centipedes determination and also Garay I. for kind help in statistical interpretation are greatfully acknowledged. Thanks to Niovi Lynghiari and C. Lionel-Marie for editorial work and manuscript typing.

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QUESTIONS and COMMENTS

G. KLEE: Did you find any physically damaged or dead larger macroarthropods in the heavily walked over areas in Row 1 or Row 2, that appeared to be injured by being stepped on?

S. MOLFETAS: The damages, in individuals with a length of 5 mm is very difficult to be identified. In any case, our method was not the hand sorting sampling but the ex--traction in Berlese-Tullgren, so that the already dead animals could not be extracted.

MS. R. SNIDER: In casual sampling near the established rows, did you frequently find isopods? What was (were) the species?

S. MOLFETAS: During the whole sampling period we have never found any isopods in this section. Nevertheless in adjacent section of the forest, with similar vegetation structure, but not trampled, we can find easily "normal" densities of isopods. The same happens also with the control (Station Biologique de Foljuif).

B.STEVENSON: The presence of undisturbed litter appears to be important for a stable macroarthropod community. Does the importance of this litter habitat for arthropods rest primarily in its structure, energy or food value, or effect on soil-litter microclimate?

S. MOLFETAS: The structure and function of the macroarthropod communities in the soil, is related with the litter's structure, because it is in the same time the habitat and the food factor, for the decomposers, which are the prey of predators' populations. So the abundance of litter, determines more or less the macroarthropods' densities.

K. RICHTER: No mention was made of pulmonate mollusks in your study: Is this an indication they were never observed and therefore not present in the Forest of Fontainbleau?

S. MOLFETAS: Three slugs were observed during the study and therefore slugs were not considered as important indicators of trampling effect.

SOIL MITE COMMUNITIES IN THE POOREST ENVIRONMENT UNDER THE ROADSIDE TREES

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**Tohoku Dental University
Japan

INTRODUCTION

In the central part of large cities wholly laid with asphalt, we can see soil surface only around roadside trees. The areas of about 1 X 1 m suare are mostly naked or covered by poorly grown weeds and the soil is very firm almost without organic layer. Such an environment seems to be one of the most unsuitable places to live for most of soil animals.

The present study was carried out in and around Yokohama City to ascertain whether soil mites inhabit such an environment or not and, if they do, what kind of species or group of mites can live there and how the soil mite communities differs from those of green area.

METHODS

The city of Yokohama is located south of Tokyo and the second largest city of Japan, having a large population of about 2,752,000(6454/km^2). The sampling was made in May, 1978 at 18 points in three serieses along the Route 16(Figure 1). The series A was taken from soils around roadside trees in the urban area near the center of Yokohama City. The series B was also taken around roadside trees, but in the suburban area outside the city. The series C was taken in green areas in and outside the city, namely in parks or groves situated not so far from the Route 16. At each point ten samples of 100 cc soil were taken by the sampler of 5 X 5 X 4 cm from around ten trees.

RESULT AND DISCUSSION

The five groups of soil mites

An unexpectedly large number of soil mites were collected from any of the three different environments. They

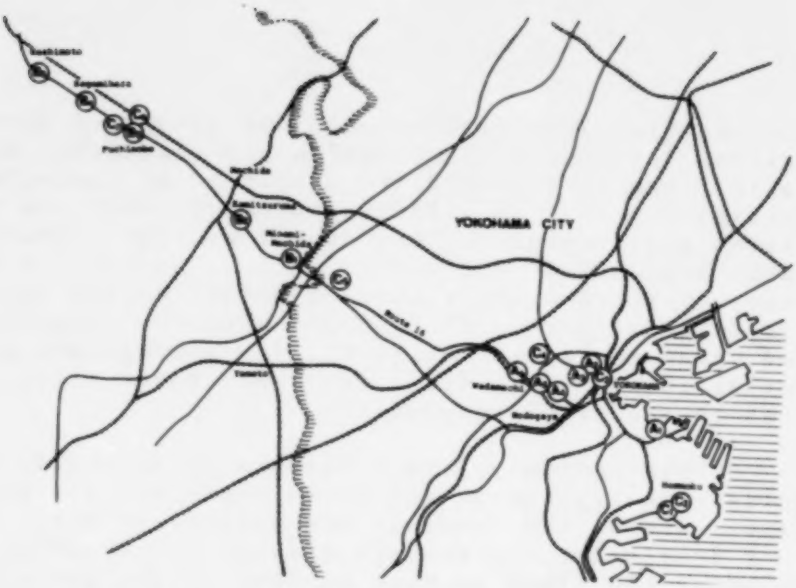


Figure 1. A map showing the sampling points along the Route 16. A_1-A_6:Urban roadsides(in the city). B_1- B_5: Suburban roadsides(outside the city). C_1- C_7:Green areas.

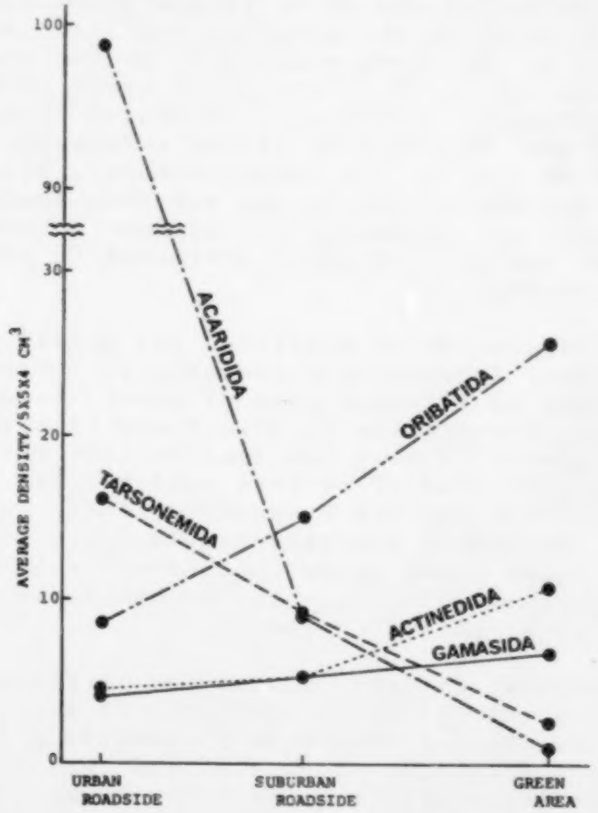


Figure 2. Change in average density of the five groups of soil mites in the three different environments.

were classified into five taxonomical groups — Gamasida, Oribatida, Actinedida, Tarsonemida and Acaridida. As shown in Table 1 and in Figure 2 the densities of Gamasida and Actinedida were not so clearly different among the three different environments, though their average numbers become slightly higher from the series A to C. However, a distinct tendency of increase in number of Oribatida was observed in the green areas(series C) compared with the suburban(series B) and urban roadsides(series A). The average density of Oribatida in the green areas was about three times as high as that in the urban roadsides.

On the contrary, the densities of Acaridida and Tarsonemida were highest in the urban roadsides and lowest in the green areas. The tendency was especially striking in the case of Acaridida, its average density in the urban roadsides being 100 times as high as that in the green areas.

A similar tendency was observed in the comparison among relative abundancies(%) of the major groups of soil micro-arthropods including Collembola(Figure 3). The average density of Oribatida was 30.9% in the green area, but it decreased to 23.6% in the suburban roadsides and was reduced to only 5.6% in the urban roadsides. On the contrary, Acaridida occupied only 1.5% in the green areas, 9.8% in the suburban roadsides, but strikingly increased to 48.9% in the urban roadsides. Tarsonemida showed a tendency somewhat different from that of the actual density, reaching to the highest percentage(16.3%) in the suburban roadsides. Relative abundancy of Collembola was highest in the green areas (34.6%), but not so strikingly decreased in the roadsides (25.1% and 20.0%).

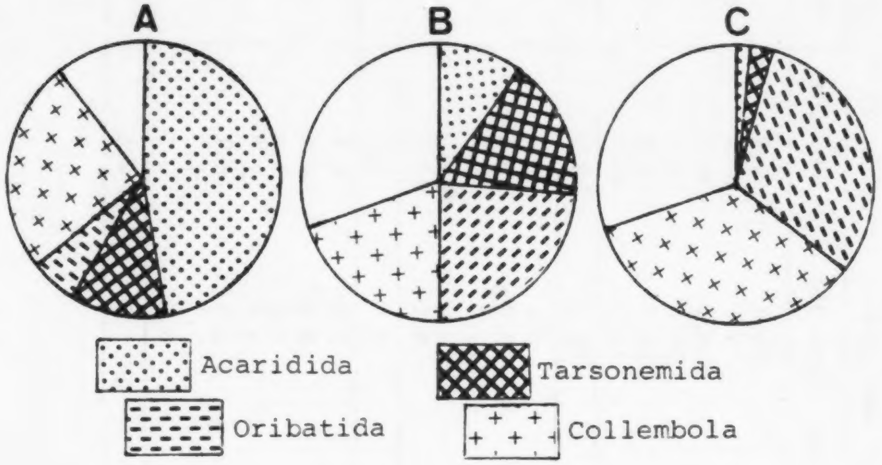
The population of Acaridida was mostly composed of a single species, Tyrophagus putrescentiae (SCHRANK), which is known in Japan as a famous pest of stored foods and "tatami" (straw mats). The species is also found in forest soils of Japan, but always in very low density. The mites of Tarsonemida mostly consisted of several unidentified species of the families Scutacaridae and Pyemotidae. These two groups of soil mites, Acaridida and Tarsonemida, seem to prefer environments under heavy human impacts and may be considered as "anthrophilic" animals, while Oribatida as a whole may be called "anthrophobic" animals.

In natural forests of Japan or in places under light human impacts, the order in abundancy of the five groups of soil mites is usually Oribatida > Gamasida ≷ Actinedida > Tarsonemida = Acaridida. It was proved that this order was converted in environments under heavy human impacts as Oribatida > Tarsonemida = Acaridida > Gamasida = Actinedida in the suburban roadsides or Acaridida > Tarsonemida > Ori-

Table 1. Density(number/5x5x4 cm^3) of the five different groups of soil mites in urban roadside(A), suburban roadside(B) and green area(C) of Yokohama.

Sampling point		Gamasida	Actinedida	Oribatida	Acaridida	Tarsonemida	Total
Urban roadside	A1 Yamashita-cho	3.6	5.0	5.6	26.3	1.9	42.4
	A2 Tsuruma	2.8	1.2	11.8	104.1	20.4	140.3
	A3 Sengen-cho	8.6	11.9	17.3	218.1	34.6	290.5
	A4 Miyata-cho	0.9	3.2	2.0	36.8	15.4	58.3
	A5 Hodogaya	5.7	4.2	6.0	181.8	28.1	225.8
	A6 Kamihoshikawa	2.6	0.7	8.0	26.2	11.0	48.5
	Average	4.0	4.4	8.5	98.9	18.6	134.3
Suburban roadside	B1 Minami-Machida	2.3	1.7	13.8	0.1	1.6	19.5
	B2 Kami-Tsuruma	12.1	3.0	10.4	13.8	5.6	44.9
	B3 Fuchinobe	4.6	4.5	8.5	21.8	11.4	50.8
	B4 Sagamihara	6.8	11.6	35.6	8.6	14.6	77.2
	B5 Minami-Hashimoto	0.9	5.7	6.1	0.1	12.7	25.5
	Average	5.3	5.3	14.9	8.9	9.2	43.6
Green area	C1 Sankei-en	8.6	7.9	15.3	2.5	0.1	34.4
	C2 Sankei-en	10.1	15.3	45.4	0.5	1.6	72.9
	C3 Yokohama Station	10.5	9.8	24.9	1.2	5.9	52.3
	C4 Yokohama Natn. Univ.	4.3	12.4	23.2	0.4	7.2	47.5
	C5 Kami-Kawai	3.2	6.1	11.9	1.6	0.1	22.9
	C6 Sagamihara	8.6	15.1	39.1	0.7	1.9	65.4
	C7 Sagamihara	1.9	7.3	20.2	0.1	0.4	29.9
	Average	6.7	10.6	25.7	1.0	2.5	46.4

Figure 3. Comparison among relative abundancies of soil micro-arthropod groups in the three different environments. A : Urban roadsides, B : Suburban roadsides, C : Green areas. The blank areas indicate the total percentage of the other micro-arthropods including the remaining mites, araneids, crustaceans, myriapods and the other insects.



batida = Actinedida = Gamasida in the urban roadsides.

The average density of total soil mites was highest in the urban roadsides, being about three times as high as that in the suburban roadsides or the green areas. Before our investigation, we supposed that the mite density would be very low in the urban roadsides and never expected such a high density which was attributed to a great number of acarid mites.

Analysis of oribatid communities

As stated above, Oribatida as a whole was found to be "anthrophobic" animals. But, are they all anthrophobic ? To elucidae the problem, the species composition of Oribatida was investigated at each sampling point.

A total of 91 species of Oribatida were found, 22 species from the urban roadsides, 37 species from the suburban roadsides and 76 species from the green areas. A part of the species showed characteristic pattern of appearance in relation to environmental difference as shown in Table 2. Oppia tokyoensis AOKI , Oribatula sakamorii AOKI and Eremulus sp.B of the "group 1" were more frequently found in the roadsides(A and B) and considered to be "anthrophilic" species. Oppia tokyoensis had been described from the soil under roadside thicket in the central part of Tokyo(AOKI ,

Table 2. Grouping of the oribatid species according to their appearance in the three different environments. The figures in the table indicate the degree of average density/100 cc soil divided into five classes — 1:0.1-0.9, 2:1.0-1.9, 3:2.0-2.9, 4:3.0-4.9, 5:5.0-14.6.

Group	Oribatid species	Urban roadside						Suburban roadside					Green area						
		A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5	C6	C7
1	Oppia tokyoensis AOKI	2	1	1	1	1	5	1	4	1	4	1	1		2				
	Oribatula sakamorii AOKI	1		4		1		1			1		2						
	Eremulus sp.B		1	2		1		3				1							
2	Cultroribula lata AOKI													3	1	5	4	5	4
	Metrioppia sp.A													3	2	1	1	3	
	Fissicepheus clavatus (AOKI)													1	1	1		1	
	Microzetes auxiliaris GRANDJEAN												1			1		1	1
	Eremobelba japonica AOKI													1	2		2		1
	Multioppia brevipectinata SUZUKI														2	1	1		
	Gymnobates sp.													1	1				1
	Eohypochthonius crassisetiger AOKI												1			1			1
3	Hypochthoniella minutissima BERLESE										1				1	1		1	
	Machuella ventrisetosa HAMMER										1	1			1	1		1	1
	Eohypochthonius parvus AOKI									1	1		1			1		1	1
	Rhysotritia ardua (C.L.KOCH)					1					1			1	1	1	1	1	1
	Oppiella nova (OUDEMANS)	1					2		1	1	1			1	5	1	3	4	2
4	Tectocepheus velatus (MICHAEL)	2	1	2		1		1	3	2	4	1	3	1	4	1	1	3	
	Oppia sp.33	2	5	5	1	4	1	5	3	2	1	4			1	3	1		
	Oppia sp.1		1	1			1	1	1	1		1	1		1	1	1	1	
	Quadroppia quadricarinata (MICHAEL)			2	1	1				1	3	1	1	1		1		1	
	Average total number	5	12	14	2	6	8	13	8	7	32	6	21	13	36	20	11	37	11
	Total species number	5	10	14	6	9	6	13	8	13	26	11	22	20	31	26	19	24	20

1974) and Oribatula sakamorii had been collected for the first time in a greenhouse of melon fruit(AOKI, 1970) and was later found from poor secondary grasslands and farms.

But, such species are rather exceptional among the oribatids. Most of the oribatid species do not like to inhabit poor soil environments under heavy human impacts. The species of "group 2" and "group 3" in Table 2 are normal in this sense, inhabiting only or mostly the green areas. The species of "group 4" are non-selective inhabitants which appeared evenly in the three different environments.

CONCLUSION

According to our expectation, the mite group Oribatida decreased in number in the suburban roadsides and more strikingly in the urban roadsides. Gamasida and Actinedida showed a similar tendency. It is incorrect, however, to say that all the soil mites decrease in soils under heavy human impacts. Acaridida and Tarsonemida were more abundant in the roadsides than in the green areas, reaching to the highest number in the urban roadsides which seem generally to be the poorest environment for soil animals. We may call these groups of mites "anthrophilic". Even in Oribatida a few species were found to be anthrophilic.

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SESSION IV: RELATIONSHIPS OF SOIL ORGANISMS TO AGRONOMIC PRACTICES AND ANIMAL WASTES

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Heterodera avenae Woll. (NEMATODA: TYLENCHIDA), THE CEREAL CYST NEMATODE: RELATIONSHIPS BETWEEN ITS POPULATION DENSITY, WHEAT GROWTH AND YIELD, AND SOIL VARIABILITY IN SOME SOUTH AUSTRALIAN WHEAT FIELDS

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INTRODUCTION

The cereal cyst nematode, Heterodera avenae Woll., also known as the oat cyst nematode, infects the roots of cereals and many other graminaceous plants in many parts of the world (see Meagher, 1977). In Australia it is widespread in the southern cereal-growing areas of South Australia, Victoria and New South Wales. Because wheat is the most widely grown and economically the most important cereal crop in southern Australia that is parasitised by H. avenae, much work has been done there on the effects of this nematode on wheat growth and production (Davidson, 1930; Millikan, 1938 a,b; Wallace, 1965; Meagher, 1968; Barry, Brown and Elliott, 1974; O'Brien and Fisher, 1974; and others).

In South Australia about two million hectares are sown to cereals each year, and about 50 to 60% of this area is sown to wheat; cereal production provides an annual gross income of about Aust. $210 million, or about 30% of the total value of farm production in the state (data from Leonard (1978) for the five years 1972-3 to 1976-7). Cereals are sown after rains in late autumn, and hatching of H. avenae in the soil is apparently controlled by falling soil temperatures and increasing soil moisture, so that the infective larvae are active in the soil in large numbers when cereal root growth begins.
Second-stage larvae emerge from cysts in the soil (mainly in the top 10cm), and enter the seminal roots of wheat plants close to the growing tip. They may survive only a few weeks in the soil unless they are able to gain entry to a root (Davies and Fisher, 1976). Hatching and emergence of larvae continue into winter, until about the end of July, and larval entry into roots continues into August.

Following infection, the plant produces giant cells (syncytia) at the infection point, and the larvae feed on the contents of these cells. The mechanism that incites development of syncytia is not understood, and would repay careful investigation, because the larvae are dependent on their formation for their further development, and an understanding of their genesis and growth might lead to a better understanding of the effects and possible control of some plant parasitic nematodes. Growth of the infected root tip ceases, and the root branches above the infection point. In cases of very heavy infection, the new root tips are infected, and this may be repeated, with further branching, producing a "knotted" system of short branching roots.

Larvae develop within the root to become adults. Adult females are spherical and remain within the root, protruding slightly onto the root surface; adult males are worm-like and emerge and move along the root surface, and after locating and fertilising the females, they die. After fertilisation the body of the female becomes progressively more distended with eggs, developing into a white ovoidal projecting body, about 0.5mm in diameter, on the root surface. This stage is known as the "white cyst", though it is really the living female; it is firmly attached to the root and is easily identified. As the plants mature the females die, but their outer cuticles remain to form brown "cysts", each containing from about 100 to about 600 eggs. The "cysts" remain in the upper layers of the soil, and in the next autumn and winter about 50 to 60% of the larvae emerge. Eggs that do not hatch in the first year may remain viable, to hatch in subsequent years; "cysts" may contain viable eggs for 10 years or more.

Counts made of "white cysts", at about the flowering stage of the plants, are generally accepted as a reliable measure of infestation rate in assessing the effects of H. avenae on plant growth and grain yield (e.g., Southey, 1956; Meagher and Brown, 1974). In our 1977 and 1978 sampling, which provided the data used in this paper, we accepted "white cyst" counts as a valid basis for assessment of the possible effects of H. avenae on wheat growth and yield, and all estimates of H. avenae populations in this paper are so based. Because we have been unable to demonstrate any consistent relationship between this measure of infestation and plant growth and yield data, we have extended our sampling in the 1979 season to include estimates of "cysts" and larvae in soil, and of larvae and "white cyst" numbers in plants from seed sowing to harvest.

Many authors have concluded that H. avenae reduces plant vigour and grain production, and efforts have been made to reduce its apparent effects by breeding resistant or tolerant varieties, use of nematicides to reduce nematode populations, and thus infection rates, and crop rotations designed to deprive the nematode of a suitable host for one or more years between cereal crops (see review of Kort, 1972). Much recent work in South Australia and Victoria has compared nematicide-treated wheat plots with non-treated controls and has attributed increased growth and yield in the treated plots to control of H. avenae (e.g., Rovira, 1978).

H. avenae is highly aggregated in its distribution and population density varies widely within small areas. We have taken whole farmers' wheat fields as sampling sites, and have designed our sampling programme to cope with the variability in H. avenae populations, wheat growth and yield, and soils so that we can make a statistically-based assessment of the relationships between them.

We have not interfered with normal farm practice nor introduced any experimental treatments, but have attempted to sample the fields, which are the units of the farmers' cropping systems. By sampling at the same points in these fields in successive crops of wheat through a crop rotation cycle we also hope to learn whether the patterns of nematode aggregation and any effects they may have on wheat growth are consistent from crop to crop.

Severe "patchiness", i.e. patches of yellowing and stunted growth, in cereal crops has long been associated with patchy infestation by H. avenae in southern Australia and elsewhere (Davidson, 1930; Hickinbotham, 1930; Duggan, 1961; Meagher, Brown and Rovira, 1978). Similar "patchiness" is also attributed to other diseases and to variability in nutrient or water availability, related to patterns of soil variability. There is little quantitative data that would relate H. avenae infestations directly to patchy growth, so we included in our study a wheat field known to be heavily infested with H. avenae, and with severe "patchiness".

METHODS

In the 1977 season three wheat fields were selected, at Coonalpyn, Bute and Calomba, in South Australia. On these fields, whose areas were approximately 30ha, 40ha and 40ha respectively, stratified-random sampling grids (50 points per field) were established, and samples of wheat plants (10 in a row per sampling point) were taken when H. avenae was at the "white cyst" stage (flowering stage of the plants) and again at harvest. Soil cores (to 1m depth) were taken at each sampling point (50 cores per site), soil profiles were described and soil samples were taken for analysis.

The fields sampled in 1977 were not sown to wheat in 1978. Two, at Coonalpyn and Calomba, have been sown to wheat again in 1979, and sampling is in progress at exactly the same points.

In the 1978 season we sampled a wheat field at Moorlands, in South Australia, that was known to be heavily infested with H. avenae, and which displayed extreme "patchiness". On a transect approximately 200m long there were three "good-growth" patches and four "poor-growth" patches; sampling points were selected on the transect mid-way across each of these seven patches. Ten adjacent plants along a row were collected at flowering stage from each sampling point; nine weeks later, immediately before harvest, a further 10 plants were collected from each of two adjacent rows at the same sampling points.

For all samples, "white cyst" counts and a range of plant characteristics were measured on each plant at the first sampling; at the second (harvest) sampling all measurements were repeated on each plant, except cyst counts and root measurements, which are not practicable when the plants are mature. The ten plants from each sampling point, at each sampling time, were dried and ground for chemical analysis, separating grain from straw at the second sampling.

For the H. avenae cyst counts and all plant measurements we aimed to collect sufficient data such that the standard errors of means should be no more than 10% of the means. Although 500 plants were collected at each of the Coonalpyn, Bute and Calomba sites, it was found that, except at the Calomba site, 300 sets of measurements were adequate for "white cyst" counts and measurement of seminal root length. At the Calomba site, 63% of plants sampled had zero counts for "white c ysts", so the cyst counts were not suitable for statistical analysis.

RESULTS

In our treatment of the data, we aimed to identify:

a. the effects of H. avenae on (i) plant mortality, (ii) plant growth, and (iii) grain yield;

b. variations in the above, related to soil variation;

c. within-site and between-site variation in nematode populations and their relationships to the above.

Some of the basic data from the sites at Coonalpyn, Bute and Calomba are summarised in Table 1. The 1977 growing season was unusually hot and dry, and grain yields were low throughout the South Australian cereal-growing areas. When plants are under moisture stress, it is believed that they are more likely to suffer severe damage from H. avenae infestations than when they have adequate moisture for growth (Barker and Olthof, 1976).

Tables 2 and 3 list correlation coefficients between data sets for Coonalpyn and Bute respectively. Where correlations include "white cyst" counts or seminal root length only those 300 plants for which data were obtained are included. For correlations between measurements made at the first and second sampling times, means of ten plants at each sampling point were used, because the plants sampled at the second sampling were not the same plants as at the first sampling. For the numbers of plants sampled correlation coefficients > ca0.25 are statistically significant ($P<0.05$), but it must be appreciated that at this level only about 6% of the variance is accounted for. Levels of significance of the correlation coefficients are given in the tables.

Twelve subdivisions of principal profile forms (classification of Northcote, 1974) were recognised among the soils at the 50 sampling points at the Coonalpyn site. Of these, 16 were solodic soils (Dy soils in Northcote, 1974) and 18 were sandy calcareous soils with gradational texture profiles (Gc soils in Northcote, 1974). Taking these two groups separately, "white cyst" counts in the Dy soils were

TABLE 1. *Heterodera avenae* "white cyst" counts and some other measurements made on wheat plants in three South Australian wheat fields in 1977. (All means ± S.E.)

(n.s.d. - no significant difference between means)

Locality	Coonalpyn	Bute	Calomba
"White cyst" counts (300 plants)			
Mean no./plant	68.9±3.6	51.7±2.7	3.75±0.78
Range	0-324	0-286	0-158
Inter-plant spacing (500 plants)			
Mean at first sampling (cm)	7.13±0.41) n.s.d.	4.12±0.23) n.s.d.	5.38±0.27) n.s.d.
Mean at second sampling (cm)	7.31±0.28)	4.71±0.34)	5.08±0.27)
Shoot height (500 plants)			
Mean at first sampling (cm)	36.8±0.37	27.7±0.72	34.5±0.81
Mean at second sampling (cm)	45.6±0.40	32.7±0.43	37.7±0.37
Shoot dry weight (500 plants)			
Mean at first sampling (g)	0.92±0.04	0.32±0.02	1.27±0.06
Mean at second sampling (g)	39.85±2.53	6.62±0.38	18.15±1.09
Seminal root length (300 plants)			
Mean at first sampling (cm)	1301.5±57.9	377.2±23.0	668.3±38.5
Nodal root length (300 plants)			
Mean at first sampling (cm)	65.4±2.7	15.0±1.6	60.0±2.5
Grain Yield (500 plants)			
Yield (g/m of row)	24.4±1.8	8.1±0.7	14.8±0.9
Estimated total yield (t/ha)	1.2	0.40	0.71
Farmer's Yield (t/ha)	1.0	0.35	0.60

TABLE 2. Correlation coefficients between some measurements of wheat plants and H. avenae "white cyst" counts, sampled at flowering (first sampling) and at harvest (second sampling) of the plants, at Coonalpyn, South Australia, in 1977.

		First Sampling						Second Sampling		
		Plant spacing	Shoot height	Shoot dry weight	Seminal root length	Nodal root length	"White cyst" count	Plant spacing	Shoot height	Shoot dry weight
First sampling	"White cyst" count	0.01	-0.58***	-0.59***	0.47**	-0.49**				
	Sem. root penetration	0.02	0.16	0.22**	0.52***	0.27*	0.13			
Second sampling	Plant spacing						0.01			
	Shoot height		0.39*				-0.23			
	Shoot dry weight			0.45**			-0.23			
	Grain yield		0.46**	0.36**	-0.05	0.29	-0.16	-0.07	0.83***	0.97***

*Pearson's correlation coefficient, significant at P<0.05, **significant at P<0.01, ***significant at P<0.001.

TABLE 3. Correlation coefficients between some measurements of wheat plants and *H. avenae* "white cyst" counts, sampled at flowering (first sampling) and at harvest (second sampling) of the plants, at Bute, South Australia, in 1977.

		First sampling						Second sampling		
		Plant spacing	Shoot height	Shoot dry weight	Seminal root length	Nodal root length	"White cyst" count	Plant spacing	Shoot height	Shoot dry weight
First sampling	"White cyst" count	-0.02	-0.13	-0.04	0.44**	0.04				
	Sem. root penetration	-0.02	0.25*	0.24*	0.24*	0.25*	-0.05			
Second sampling	Plant spacing						-0.02			
	Shoot height		0.69***							
	Shoot dry weight			0.52**						
	Grain yield		0.68***	0.59**	-0.21	0.52**	-0.36*	0.00	0.86***	0.92***

*Pearson's correlation coefficient, significant at P<0.05, **significant at P<0.01, ***significant at P<0.001.

much lower (mean=59.2 ± 5.6 per plant) than in the Gc soils (mean=94.6 ± 5.4 per plant), and this difference is significant ($P<0.05$), but the mean grain yields were 22.7 ± 2.8 and 23.2 ± 3.2g/m of row length, and these means are not significantly different. At the Bute site six primary profile forms were recognised at the 50 sampling points, and of these 35 were sandy calcareous soils with gradational texture profiles (Gc soils). Mean "white cyst" counts per plant in the Gc soils were 48.5 ± 2.8, compared with 53.0 ± 7.5 for all other soils and 51.7 ± 2.7 for all 50 sampling points, while mean grain yield was 9.1 ± 0.8g/m of row length, compared with 8.1 ± 0.7g/m of row length at all 50 sampling points. In none of these pairs of figures is there any significant difference.

Some results for the "patchy" wheat field at Moorlands are presented in Table 4. "White cyst" numbers per plant in the "poor-growth" patches were about 11 times those in the "good-growth" patches, and this difference was significant ($P<0.001$). Shoot dry weight per plant in "poor-growth" patches was about half that in "good-growth" patches, and this difference was significant ($P<0.05$). The total length of the seminal roots per plant at the flowering stage was much greater in the "poor-growth" patches than in the "good-growth" patches, and this might best be interpreted as a reflection of a difference in soil fertility between "poor-growth" and "good growth" patches, with the plants in the "poor growth" patches being forced to explore a greater volume of soil to obtain nutrients because of lower fertility than in the "good-growth" patches. It is of interest that there were much greater numbers of H. avenae cysts on the longer roots in the "poor-growth" patches than on the shorter roots in the "good-growth" patches, and that the difference in root length was significant ($P<0.05$); in both sets of plants seminal root length was positively correlated with numbers of "white cysts" and the correlation coefficients were significant ($P<0.001$). Figures for grain yield in good- and poor-growth patches are not easily interpreted. It is not possible to make correlations for these data on a plant-by-plant basis, as with other data in Table 4, because the plants taken at harvest were not the same individuals as those taken at flowering, so only the mean values at each sampling point of the plant and nematode data can be used and the data sets are very small. However, taking the mean values for grain yield in g/plant, the plants in the "good-growth" patches apparently produced about twice as much grain as those in the "poor-growth" patches, and this difference was significant ($P<0.05$), but in neither case was the grain yield significantly correlated with mean "white cyst" counts for adjacent plants at flowering stage. If the grain yield is recalculated as g/m of row length, which gives an indication of the real-world production of the crop, the mean yield in "good-growth" patches was no longer significantly different from that of the "poor-growth" patches; at the same time, the yield in both sets of plants now became negatively correlated ($P<0.001$) with "white cyst" counts previously made on adjacent plants at flowering stage, and the correlation apparently accounted for a high proportion of the variance.

TABLE 4. *Heterodera avenae*: seminal root "white cyst" counts and some other measurements from wheat plants in good and poor-growth patches of a wheat field at Moorlands, South Australia, in 1978

	Good-growth patches		Poor-growth patches		All plants	
	Mean ± S.E. (Range	$r^{\dagger}$ (r^2)	Mean ± S.E. (Range)	$r^{\dagger}$ (r^2)	Mean ± S.E. (Range)	$r^{\dagger}$ (r^2)
Seminal root "white cyst" counts (no./plant)	5.44±1.13 (0-80)		60.84±4.29 (14-133)		36.69±3.98 (0-133)	
Shoot dry weight (g)						
a. at first sampling	1.91±0.23 (0.13-5.35)	0.48** (0.28)	0.77±0.08 (0.10-2.75)	0.18 (0.03)	1.28±0.13 (0.10-5.35)	-0.34** (0.11)
b. at second sampling	5.66±0.49 (0.30-18.71)	-0.19 (0.04)	2.60±0.27 (0.08-13.24)	0.01 (0.00)	3.93±0.29 (0.08-18.71)	-0.27** (0.07)
Seminal root length at sampling (cm)	402.7 ±63.2 (57-1937)	0.56*** 0.31)	803.0 ±75.9 (104-2060)	0.54*** (0.29)	637.4 ±54.8 (57-2060)	0.61*** (0.37)
Grain yield						
a. g/plant	2.17±0.18 (0.29-8.16)	-0.69 (0.48)	1.10±0.11 (0-4.30)	-0.21 (0.04)	1.57±0.11 (0-8.16)	-0.75* (0.56)
b. g/meter length of row	36.33±7.99 (20.11-53.92)	-0.99*** (0.98)	21.92±5.67 (13.52-41.28)	-0.84* (0.71)	28.10±5.43 (13.52-53.92)	0.26 (0.07)

†=Pearson's correlation coefficient for correlation with seminal root "white cyst" counts
*=Correlation coefficient significant at $P<0.05$, **significant at $P<0.01$; ***significant at $P<0.001$.

DISCUSSION

Sampling involves destruction of the wheat plants, and it must therefore be assumed that measurements made on plants taken at the flowering stage (first sampling) can legitimately be compared with adjacent plants taken at harvest (second sampling). That this requirement has probably been met in this investigation is indicated by the significant positive correlations between shoot height and also plant dry weight at the first sampling and these same measurements made on plants at the second sampling (Tables 2 and 3).

There is no evidence that H. avenae caused significant plant mortality; if it did, there should have been a significant negative correlation between "white cyst" numbers per plant and spacing between the plants (Table 1), and this was not apparent either at the first or at the second sampling (Tables 2 and 3). Grain yield does not correlate with plant spacing within the limits of spacing found in the fields we sampled; within practical limits, plants that are more widely spaced apparently grow larger and produce more grain than more closely spaced plants (see Tables 2 and 3).

At the Coonalpyn site there was a significant negative correlation (Table 2) between "white cyst" counts and plant dry weight at the flowering stage, and this may be interpreted as indicating that H. avenae causes a check to early growth of the plant. No such evidence was available at Bute (Table 3), and at neither site was there any evidence of this effect by the time the plants were mature.

There was a significant negative correlation between "white cyst" counts and grain yield at Bute, but no such relationship was shown by the Coonalpyn data. "White cyst" counts ranged from zero to several hundred per plant (a very heavy infestation) at both sites, so it was possible to examine a wide range of possible interactions. Two sets, each of 50 plants from five sampling points, along lines at right angles to each other across the middle of the Bute field, were examined separately. In one of these sets of five points mean "white cyst" counts were 75.7±7.5 per plant and in the other set they were 68.0±10.28 per plant (no significant difference). Grain yield in the two sets was 8.7±1.4 and 5.3±0.6g/m of row length respectively (no significant difference). However, the correlation coefficients for the relationship between "white cyst" count per plant and grain yield per plant were respectively -0.81 and +0.88, and these results are significant ($P<0.05$ and $P<0.01$ respectively). It must be concluded that in at least one, and perhaps in both cases, these correlations do not reflect cause and effect relationships.

At Coonalpyn, Bute and Moorlands (tables 2,3 and 4) we found significant positive correlations between total length of seminal roots and "white cyst" counts on the seminal roots, i.e., the more roots the more "white cysts". The principal effect of H. avenae on plant growth and yield is generally claimed to derive from the stunting of the seminal roots, which reduces their depth of penetration in the soil, resulting probably in reduced water and nutrient uptake by the plant, and eventual reduction in yield. In addition to measuring the total length of the seminal roots, we also measured the seminal root penetration, i.e., the length of the longest seminal root, on all plants at the flowering stage, when we also counted the number of "white cysts" on the same sets of seminal roots. There was no significant correlation between this measure of seminal root growth and seminal root "white cyst" counts at Coonalpyn or Bute, the only sites where we were able to make statistically reliable estimates (r=0.13 and -0.05 respectively). The same correlation was done separately for Gc and Dy soils at Coonalpyn, where Gc soils had much higher "white cyst" counts than Dy soils, but again there was no significant correlation (r=-0.02 and 0.14 respectively). Also, despite the much higher "white cyst" numbers of plants growing in Gc as compared with those growing in Dy soils, the mean root penetration at flowering stage for plants on Gc soils was 14.4±0.6cm and on Dy soils 13.8±0.6cm, and these means are not significantly different. This is not to deny that H. avenae infestation may result in reduced seminal root penetration into the soil, because there is much evidence that it does so (e.g., Holdeman and Watson, 1977). It is more likely that variation in depth of penetration of seminal roots is due to a number of factors, including variations in soil type, micro-topography (influencing soil moisture), fertiliser application, and probably many other things, and that H. avenae infestation level, except in extreme cases, is not the most important factor, or even a very important factor, in regulating the depth of seminal root penetration in the overall picture of a farmer's wheat field. The depth of seminal root penetration was significantly positively correlated with shoot dry weight, total seminal root length, and length of nodal roots at flowering stage, at both Coonalpyn and Bute, and also with shoot height at that stage of growth at Coonalpyn (Tables 2 and 3); it is apparently a fairly significant indication of the general health of the plant at that stage. When the mean seminal root penetration at flowering stage was compared with grain weight at harvest of plants from the same sampling points there was no significant correlation at Coonalpyn (r=-0.02 for grain yield per metre of row length; r=-0.04 for grain yield per plant), but at Bute there was a significant positive correlation (r=0.52** and r=0.46** respectively). Apparently the plants at Coonalpyn, which eventually grew much larger (about six times the weight) and yielded about three times as much grain as those at Bute (Table 1), had recovered from the early check to growth, while those at Bute had not recovered.

Data from Coonalpyn indicate that a contrast in soil types may be reflected in a significant difference in "white cyst" counts, as the sandy calcareous (Gc) soils had higher counts than the solodic (Dy) soils. The difference may be due to different texture and drainage characteristics of the soils, affecting larval motility and survival, but we have no evidence to support this, and it may be that in another season, with different weather conditions and soil moisture relationships, the effect would be different. Despite the differences in soil and related differences in H. avenae "white cyst" numbers at Coonalpyn, there was no significant difference in grain yield between Gc and Dy soils; the farmer's cultivation and fertiliser practices must have over-ridden any differences in soil fertility between the two groups of soils.

CONCLUSIONS

The work reported here represents results from only one season's work, and some very simple statistical analyses of the data. This year (1979) a more comprehensive study is in progress, at the same sampling points, at the Coonalpyn site. At this site the H. avenae population and its relationship to the wheat plants and to soil variation is being followed from the date of sowing of the wheat right through the season until harvest. At the Calomba site sampling similar to that in the 1977 season is being repeated. It may be that significant damage is done to plants by H. avenae at an early stage, and that we did not recognise this from our 1977 sampling, which began at the flowering stage, or the "white cyst" stage of H. avenae; if this is so our conclusions from the 1977 season may be invalid, but so too will be most of the conclusions of previous workers on the effects of H. avenae on the growth and yield of cereals, since nearly all the work that has been done in the past has been based on "white cyst" counts as a valid measure of the H. avenae population, as related to cereal growth and yield.

When we have data for this season, and have completed chemical analyses of soil samples and of plant samples from the 1977 and 1979 samples, we intend to apply multivariate statistical methods to the data to try to quantify the contribution of H. avenae cyst, larval, and "white cyst" population densities to an array of factors that appear to influence the growth and yield of wheat plants.

On the basis of our results so far we conclude that, at least in southern Australia conditions:

1. there is no evidence that H. avenae causes significant mortality of wheat plants.
2. H. avenae may adversely affect wheat plant growth at an early stage, but the plants are capable, given reasonable conditions for growth later in the season, and even when infestation rates are high, of recovering so that the effect is no longer evident at harvest.
3. the major direct effect of H. avenae observed by previous workers in southern Australia and elsewhere is a reduction of the depth of penetration of the seminal roots of affected cereal plants. We have shown that reduction in depth of seminal root penetration resulted, at our sampling sites, in reduced plant growth, at least at an early stage and perhaps through to harvest, but even in wheat fields that were very heavily infested with H. avenae there is no dvidence that this nematode was a critical, or even a significant factor in regulating the depth of seminal root penetration on the scale of

variability that is found in a farmer's wheat field, with an area of 30 to 40ha.

4. the sampling methods we used and the data we obtained should be adequate to detect reductions in plant growth and grain yield of more than about 10% over-all. No such effects that could be attributed to H. avenae infestation were apparent in our results.

5. our results conflict with those of much recent work in southern Australia, especially the results of plot trials that have measured the response of wheat plants to the application of nematicides, and have attributed the measured improvements in growth and yield to control of H. avenae (e.g., Brown, Meagher and McSwain, 1970; Meagher, Brown and Rovira, 1978).

Nematicides are broad-spectrum biocides, whose effects on non-target organisms, and, for that matter, directly on plant growth, are often drastic, and in the context of work in southern Australia are virtually unknown. We conclude from our results that field experiments that compare nematicide-treated plots with non-treated plots and rely for their assessment solely on comparisons of plant survival, growth, weight, and grain yield at harvest are not capable of testing so specific an effect as that of a particular nematode (H. avenae) on wheat growth and yield.

6. difference in soils may significantly influence levels of nematode infestation on plant roots, but such differences in infestation levels were not reflected in final grain yield in our experiments.

7. "patchy" growth, which is common in southern Australian wheat fields, may possibly be due to H. avenae infestation, but our evidence shows that in a particularly severe example that we investigated, although mean H. avenae populations were much higher and grain yield was much lower in "poor-growth" than in "good-growth" patches, it was not possible to show any significant causal relationship between H. avenae "white cyst" numbers and plant performance; there is no doubt that high "white cyst" numbers and poor plant performance were co-variants, but they were not directly related.

8. an interesting philosophical question is raised by the results we have obtained. Here is a soil-inhabiting animal that, for most of its life cycle, is a parasite of the roots of cereal plants, in our case wheat plants, and we can show that at an early stage of growth of the plants the depth of penetration of their roots may be inversely related to the rate of infestation of the roots by the parasite. Reduction of early root penetration may affect the final grain production of the plant, though it seems that the plant, given reasonable growing conditions later in the season, may recover so that the effects of reduced root penetration at an early stage do not influence the final grain yield. On the scale of wheat fields of 30 to 40ha many environmental factors that affect final wheat yield are variable, and there are factors other than level of H. avenae infestation that affect the depth of root penetration. How then are we to assess the effects of a parasite of wheat roots, that is known to be very discontinuously distributed on the scale of a wheat field, and whose only known harmful effect is to reduce the depth of root penetration at an early stage of growth, in terms of eventual yield of

grain. We believe that this can be done realistically by regarding the problem as one of interactions within an ecosystem comprising the population of H. avenae, wheat plants, and soils, each of which is affected to varying degrees by many factors (see also Wallace, 1978). To make some kind of approximation to a model of such an ecosystem it is necessary first to design a sampling programme that is capable of estimating relevant attributes of the populations and variability within them, with an acceptable level of confidence, and then to use statistical methods to assess the relationships between the levels of H. avenae infestation and other factors that may determine the performance of wheat plants. This is what we are attempting to do, using methods that have been successfully used in many studies of soil animal populations, and applying them to a problem that involves parasite/host relationships in an agronomic context.

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SOIL FAUNA IN TWO VEGETABLE CROPS GROWN UNDER PLASTIC TUNNELS

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INTRODUCTION

In Egypt, Hafez (1939, 1947) investigated the insect fauna of dung. El-Kifl (1957, 1958) recorded soil fauna under various vegetations and some soil types. Tadros (1965, 1967, 1974, 1977, 1978) surveyed the fauna under some crops, green lawns, and fallow field in some districts, and recorded the effect of some ecological factors responsible for fauna fluctuations.

In association with a trial to harvest tomatoes, either as seedlings or fruits in the cold season in Egypt and to produce cucumber fruits in the early season, the following investigation was carried out with the following objectives:

1) To compare the fauna under plastic tunnels with that of the open air sites in the same area.
2) To find out the effect of growing two vegetable crops (tomato & cucumber) on soil fauna either under the same previous tunnels when they were covered by plastic in the cold season, or uncovered afterwards.
3) To compare the fauna found under a tomato crop grown under plastic tunnels with that grown in the open air.
4) To investigate the effect of some fertilizers, plant spacing and some cucumber plantations on soil fauna.

MATERIALS AND METHODS

The experiment was carried out at the horticulture farm in the Faculty of Agriculture at Kafr El-Sheikh, 130 km to the northeast of Cairo. Two parcels of land, each of 250 square metres, were selected for this purpose. It was planned to cover these two plots by a plastic covering in the shape of a tunnel by the aid of iron bars fixed to the soil during the cold season. The tunnels were supplied with doors for the control of both temperature, relative humidity and to be a way of controlling pest infestation if possible.

The first tunnel was cultivated with 21 species of tomato. Plants were grown on wires tied to tunnel tops. Every species was replicated 4 times, namely 48 plots over all the area. In everv plot 16 plants were cultivated. Every two plants were 40 cm apart.

The second tunnel was divided into equal parts. The front was cultivated with 7 cucumber species (Pecador, Belair, Kobus mix, Fakor mix, Fablo mix, Nicracross and Mirella). Each species was replicated 4 times (32 plots). In every plot 7 plants were cultivated at 40 cm apart. The rear part was cultivated with only one species of cucumber but differed in spacing (20 or 40 cm)and fertilization (NPK) that was added at 3 rates to the plot.

Samples were taken by the same way described by Tadros (1967), and extraction took place for 48 hrs in batteries of modified Tullgren funnels. The experiment lasted for 6 mo, beginning in November and ending by May of the same year.

RESULTS AND DISCUSSION

COVERING EFFECTS

Total Fauna

It was clear from the data that covering the soil with plastic created a suitable environment in which both plants and fauna flourished. Fauna nearly doubled in soil cultivated with cucumber species (35.87% to 64.13%) and was enhanced in fertilized treatments (from 26.88% to 73.12%). This result may be due to the suitable environmental factors of temperature and relative humidity (RH).

The numbers in Table 1 indicated that the cover raised both air temperature about 2°C and soil temperature about 1.5°C (at 5 cm deep) over that of the open air. It was also clear that the covering raised the RH about 0.3%. This variation in both temperature and RH may be a direct or indirect cause for the faunal increase under tunnels.

Table 1: TEMPERATURE AND RH (MEANS) DURING COLD SEASON, UNDER PLASTIC TUNNELS AND IN THE OPEN

MONTHS	Temperature		RH	
	Under plastic	In open	Under plastic	In open
January	15 C.	13.2 C.	84%	78%
February	15.2 C.	12.7 C.	76%	74%
March	15 C.	13.0 C.	78%	74%

This result was confirmed in the second tunnel cultivated with tomato. The data indicated that fauna doubled under cover (32.40% to 67.60%).

Soil Fauna Present

Four groups of fauna were extracted, namely Insecta, Myriapoda, Acarina and Oligochaeta. Acarina was further subdivided into two groups, Oribatei and the soft-bodied acarines.

The percentages presented in Table 2 show that the closed atmosphere caused the soil insects to flourish more abundantly than those in the open, since they increased about 3 times (from 73.82% to 26.18%, respectively).

Table 2: EFFECT OF COVERING ON MAIN FAUNA GROUPS

CLASSES	Covered		Uncovered	
	Mean	% Frequency	Mean	% Frequency
INSECTA	299.25	73.82	106.10	26.18
MYRIAPODA	13.00	72.22	5.00	27.78
ACARINA	14.50	40.65	21.75	60.00
OLIGOCHAETA	0.50	100.00	0.00	0.00
Total	327.25	-- --	132.85	-- --

Myriapoda gave the same result as insects, (72.22% to 27.87%). The Acarina were not so much affected in these two different atmospheric zones (60% to 40.65% in open versus covered). The authors attribute these results to the fact that this group penetrates to more than 30 cm deep (Tadros et al. 1965). Hence acarines flourish under different microclimatic strata of temperature, RH, amount of organic matter and water table; they were not affected so much by these limits. Earthworms were found to flourish under the covered area (100%) only due to the very suitable environmental conditions offered under closed atmosphere. The agricultural operations (such as harrowing and irrigating) carried out in uncovered plots may be the main reason for the escape or the death of earthworms.

SPECIFIC CROP EFFECT

The difference in cultivated vegetable crops seemed to affect soil fauna differently (Table 3). Fauna flourished under cucumber plantations either under tunnel or in the open. On the other hand, they did not flourish under tomato plants. We attribute this to the differences in types of root systems or to the various root metabolism secretions of the two selected plants (Tadros et al. 1965).

Table 3: SOIL FAUNA (MEANS) IN TWO VEGETATIONS, UNDER TUNNELS AND IN THE OPEN AIR

Vegetations	Covered	Uncovered
Cucumber Species (8)	212.13	118.63
Tomato Species (12)	37.05	17.76

OTHER AGRICULTURAL EFFECTS

Fertilizer

As indicated in Table 4 it was obvious that the higher the quantity of fertilizers added, the lower the percentage of fauna obtained. This may be attributed to the direct effect of fauna nutrients and acidity, or on the other hand, the fertilizers or their impurities may have been toxic to microflora.

The fertilizers added in this experiment (ammonia) make the soil more acid, increasing fungal growth (Hill et al. 1975) and consequently increasing fungal feeding fauna. Data showed such a rapid decrease in fauna numbers. We attribute this fact to the toxic effects of such fertilizers, or to the immigration of organisms deeper in soil immediately after fertilizers application.

Table 4: EFFECT OF FERTILIZATION RATIO (NPK) ON SOIL FAUNA UNDER TUNNELS

Spacing	Fertilization ratio					
	(A) High		(B) Medium		(C) Low	
	Mean	%	Mean	%	Mean	%
20 cm	50.75	31.42	52.50	32.50	58.25	36.08
40 cm	42.50	17.89	72.75	30.63	12.25	51.48
Total	93.25	23.37	123.25	31.49	180.05	45.24

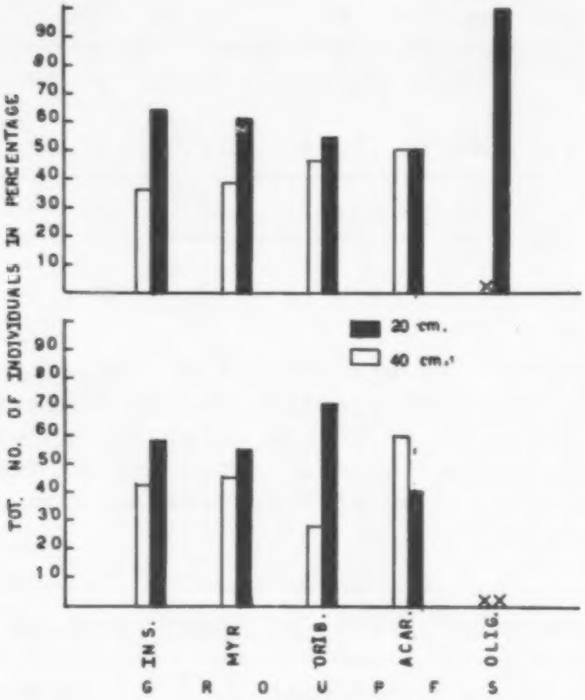
Spacing

Total fauna. It was clear from Tables 4 & 5 that the closer the plants were planted, the more the fauna flourished either under tunnels or in the outer atmosphere. This result was more clear under tunnels. This may be due to suitable environments offered by root systems as food, shelter or suitable aeration.

Table 5: EFFECT OF SPACING ON TOTAL FAUNA IN CUCUMBER

SPACING		COVERED	UNCOVERED
20 cm	Mean	248.75	83.00
	%	62.07	56.08
40 cm	Mean	152.00	65.00
	%	37.93	43.92

Soil faunal groups. The numbers as illustrated in Figure 1 indicated that nearly all groups tended to flourish with aggregated plants, except with Acarina. The variance in some groups was so clear such as with the Insecta and Oribatei. This result may thus show that both insects and Oribatei prefer soils planted with aggregated plants. The importance of oribatids is known in raising soil fertility owing to the role it plays (Tadros, 1967). Oribatei (probably organic matter feeder) flourish in soils of aggregated plants, while other acarines are not so much affected owing to their mode of living and feeding.



Fig(1): The effect of spacing on fauna groups.

Fertilizers & Spacing

It was obvious from Table 4 that aggregated plants (at 20 cm apart) did not affect fauna so much at the different rates of fertilizers. This may be due to the sufficient food in the soil, by these nearness of plants and perhaps by the unsuitable chemical environment occurring in soil after adding these fertilizers. With plants at 40 cm apart, the higher the quantity of fertilizer added, the lower the fauna obtained. This last result shows that spacing would perhaps give a way for the root system to grow and hence for the fauna to flourish.

Cucumber Species

The data indicate that the differences in fauna between the 8 selected cucumber species were small, but fauna extracted under the Kobus-mix was higher (18.29%) than the others, with Fakormix ranked second (14.74%). The other six species ranged between 10-12%. These slight differences may be due to the differences in root system form that creates a suitable environment in which fauna may flourish. This last result was assured when finding the yield highest in Kobus reaching 2.15 Kg/m^2 and least in Mirella reaching 0.80 Kg/m^2.

SUMMARY

On examining the effects on soil fauna by covering the soil during the cold season in Egypt with plastic tunnels our data showed that this new atmosphere was more suitable for both fauna to flourish and plantations to grow.

Two vegetables were grown under tunnels, namely cucumber and tomato, in order to produce their fruits for early market or to produce tomato seedlings in the cold period of the year. The mean of extracted fauna under cucumber was higher than that under tomato.

This experiment indicates that the higher rates of NPK lessened faunal percentages, while the aggregation of plants raised faunal percentages. There were some differences between the extracted groups in accordance with these two factors. The fauna was not much affected by the two vegetative species.

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BEACH SOIL MICROFAUNA IN LOWER EGYPT

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INTRODUCTION

It was of great interest to investigate the soil fauna on the seashore to get an idea about this new area especially in a town where the Faculty of Agriculture at Kafr El-Sheikh is situated. The selected town for this investigation is Baltim; it is situated about 115 km north-east of Kafr El-Sheikh and about 245 km to the north of Cairo.

Investigators working on seashore soils include Luxton (1964, 1966) who made a series of ecological investigations of the salt marsh acarina in southern Wales. Webb et al. (1971) worked on cryptostigmata occurring in a sandy heathland soil in southern England. Fujikawa (1972) recorded the results on the zonal changes of oribated fauna in vegetation of the Ishikari seashore near Sapposo, Japan, and Cancela de Fonseca (1975) studied the colonization of fresh litter by aid of fauna, algae and fungi in two soils of a beach forest in France.

In Egypt, there are no records about the seashore fauna, and therefore, the present investigation was planned to learn about the horizontal and vertical distribution of species either in non-cultivated or cultivated areas from plots beside the seashore and away from it.

METHODS AND TECHNIQUE

The research area was situated on a peninsula between the Mediterranean Sea and Borolos Lake. Cultivations were not grown regularly in the area, but one finds green plots beside sandy ones owing to the nature of the soil itself and to the total suspended solid content.

Samples were taken during the winter from six plots representative of a horizontal distribution of the whole area. These plots were scattered either close to the sea or about 0.8 km (0.5 mi) away from it. Three types of samples were taken, the first from plots close to the sea and never cultivated, the second from plots like the first but cultivated with ordinary field or vegetable crops, while the third was from orchards, some near the seashore and others 1.6 km (lmi) away from seashore. The winter crops on the second plot type were beans, wheat and alfalfa. _Ficus_ was the only plant grown in the orchards.

The sampling procedure was discribed by Tadros et al. (1965) and was representative of the vertical distribution of the soil. Samples were taken of the disturbed soil layer (0-20 cm) and undisturbed layer (20-40 cm) below. Extra samples were also taken from a plantation beside the seashore and away from it for about 2 km to represent the horizontal distribution. Extraction for 48 hrs took place using batteries of modified Tullgren funnels.

RESULTS AND DISCUSSION

Extracted Fauna Groups

From six plantations in the test area 10 different organisms were extracted; they were all arthropods and belonging to three classes, Acarina, Insecta and Myriapoda. Some species of Chelontida were collected. Collembolans were the prevalent species extracted from all the tested fields followed by _Glycophagus_ _destractor_ (Shrank). These results are similar to the findings of Dindal and Metz (1975).

Total Fauna and Cultivations

It appears that alfalfa and beans were the crop lands most preferred by soil fauna while tomato was the least (Figure 1, Table 1). Fauna were also present in fallow fields but in low percentages, except for the Acarina (82.35%). This result may be due to the crop residues left on that soil. Microflora work on the cast residues decomposing it to a grade which is favorable to microfauna. This process on cultivated lands happens without any human assistance. The different percentage of faunal group fluctuations in the six tested plots plus the uncultivated area may be due to the nature of

TEST SITES FAUNAL %	Alfalfa	Wheat	Beans	*Ficus*	Tomata	Fallow	Uncultivated
INSECTA	71.73	58.75	41.87	25.65	46.43	17.65	60.00
ACARINA	20.14	41.26	67.22	74.35	53.35	82.35	40.00
MYRIAPODA	3.53	0.00	4.55	0.00	0.00	0.00	0.00

Table 1: PERCENTAGES OF THREE FAUNA GROUPS OCCURRING IN UNCULTIVATED AND FALLOW LAND AND FIVE PLANTATIONS

	Bulk Density g/cm	Water content %	Porosity %	pH	Organic matter %	Total Fauna %
Uncultivated land near seashore	1.54	0.94	41.62	6.77	0.02	0.50
Cultivated seashore land with crops	1.72	1.62	35.02	7.60	0.90	95.60
Cultivated land with *ficus*	1.22	6.00	54.02	7.58	0.88	3.90

Table 2: ANALYSIS OF SOME IMPORTANT PARAMETERS OF THE CHOSEN SOIL NEAR THE SEASHORE

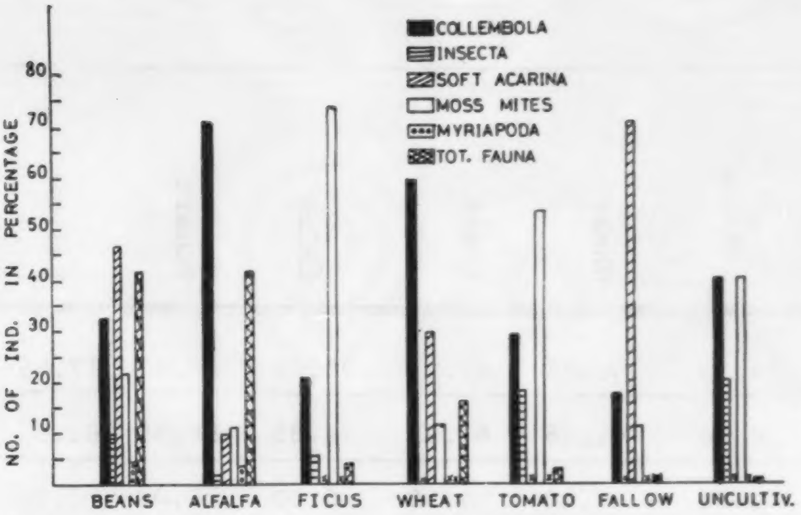


Fig.(1): Numbers in percentages of important fauna groups in five plantations, fallow & un-cultivated aera.

the different root systems of those plantations.

Bulk density; water content, porosity, organic matter and pH differed between sites (Table 2). The uncultivated land, close to seashore had a relatively high porosity, low water content and low percentage of organic matter that prevents some fauna groups from occurring. In the soil of cultivated seashore lands the Insecta were the most prevalent taxon. The percentage of organic matter and porosity had a clear effect on the faunal distribution.

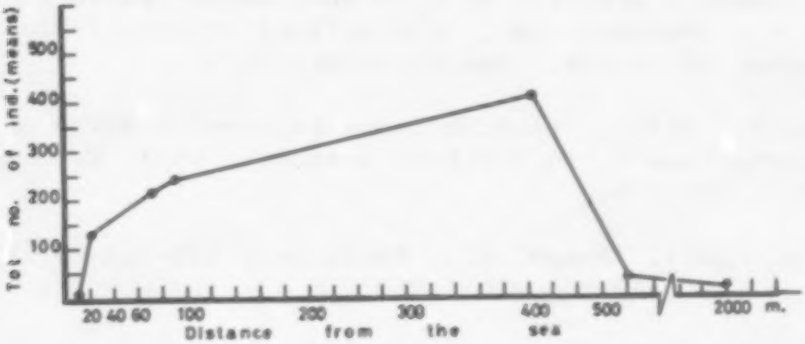
Main Fauna Groups & Cultivations

Acarina was the prevalent group in four of the seven tested sites (Figure 1), while the Insecta dominated the three remaining areas. This result is due to either springtails or Coleoptera occurring at high rates in alfalfa, wheat and in the uncultivated area. Myriapoda were present only in legume crops. This result may be due to the trophic characteristics of these animals for they eat fungi and decomposed organic matter that may be offered at high rates in the rhizosphere of the leguminous plants.

The Vertical and Horizontal Distribution of Fauna

About 70% of the fauna was extracted from the upper layer (0-20 cm) of the soil surface (Figures 1 and 2). This result may be due to the characteristics of sandy soil, its porosity, and the amount of organic matter within it, resulting from its cultivation with crops. Also, most soil fauna are fungivorous or organic matter feeders and those conditions are more prevalent in the upper soil strata.

In measuring fauna horizontal distribution (Figure 2) it was clear that the peak occurred in plots which were about 420 m from the sea. This fact may be due to total soluble salts and needs further investigation.



Fig(2): Horizontal distribution of total fauna

SUMMARY

Seven plots of land ranging from the seashore inland were selected to determine soil microfauna occurring within it. These plots were situated in a peninsula between the Mediterranean and the big Borolos Lake. In this new area ordinary crops and orchards were grown up in only some scattered plots.

All extracted organisms were arthropods. Acarina was a prevalent group in four out of the seven examined plantations. On the other hand, Insecta flourished in the uncultivated plots, while Myriopoda was extracted only in soils cultivated with legume crops. It was found that high percent-

ages of fauna flourished in the upper soil layer. The author attributed this distribution to: presence of plantations, water content, porosity, pH, and faunal interactions with microflora in the rhizosphere.

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EFFECT OF NPK COMPLEX FERTILIZERS ON YIELD OF PADDY RICE AS RELATED TO THE FAUNA AND WATER INFILTRATION RATE OF SOIL OF THE NILE DELTA

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Abstract:

Several ecological factors have been changed after the building of the Aswan Dam (1963). The annual rate of K-replenishment of Egyptian soils must have been reduced as a result of the sharp decrease (97%) in suspended matter (largely K-bearing minerals) in the Nile river. Therefore, field experiments were conducted on the alkali saline alluvial (55% clay) soil of Kafr El Sheikh, to test the effect of NH_4, urea pellets, NP and NPK viking ship complex fertilizer (from Norsk Hydro, a.s.) on grain yield of two paddy rice cultivars (Giza 172 and IR579) as well as soil fauna (insects, acarina and collembola) and rate of vertical infiltration of water. The results showed that the yield of cv. 579 was significantly higher with NPK- (454.g/m^2) than NP- (346.g/m^2) or N- treatments (308.g/m^2). Similar trend was observed with cv. 172. The yield of rice grains increased hyperbolically with increasing density of collembola up to 140/kg) further increase in collembola to 320/kg soil did not affect the yield. The density of acarina increased hyperbolically to 24/kg with increasing the dry weight yield of roots per hill. The grain yield as well as the density of collembola were negatively correlated with the infiltration rate which varied from 0.1 to 1.3 cm/min. in different treatments. At a constant N, the density of insects was found to decrease (from 20 to 4/kg) with increasing K level, this decrease was observed with cv. 579 but not with cv. 172.

Introduction:

For thousand of years floading of the Nile river resulted in the deposition of suspended K-rich clay into the soils. The process provided Egypt with an untapped source of K-replenishment. The warm Mediterranean climate prevailing in this area as well as the constant availability of irrigation water, provided elements for a very intensive agricultural system, producing two to three crops annually. About 97% of the suspended matter (Helal and Rasheed, 1976) was lost after the construction of the Aswan Dam (1963). About one fourth of the annual consumption of P was lost as a result of the construction of the Dam (Balba, 1979). Whilst the dissolved K in Nile water was unaffected by the Dam, about 91% of the annual deposition of K into the soil was lost (Balba, 1979). This situation may be aggravated by the present consumption of very high rates of N in relation to P with virtually no K. Meanwhile NH_4-N fertilizers were found to inhibit K uptake (Faizy, 1979) from the soil solution (Grimme, 1974). On the other hand the susceptibility of plants for fungus infection was highly increased at low K and high NH_4-N fertilization (Faizy, 1978). The physiological, morphological and phenoligical changes which were usually induced following fertilization were found to affect the population dynamics phytophageous insects (Bogenschutz and Konig, 1976). A decrease in the density of soil fauna was reported following fertilization (Ronde, 1957 and Beckan, 1972). Soil physical properties, such as high compactness and low permeability, were found to have a determinable effect on soil fauna (Wilcke, 1963).

Since NPK compound fertilizers have never been used in Egypt it was therefore one of the objectives of this study to compare the effect of straight N fertilizers with that of NP and NPK compound fertilizers on the yield of two paddy rice cultivars as well as their influence on the density of soil fauna and the response of soil insects to different rice cultivars. The relationship between water infiltration rate and density of collembola and grain yield was investigated.

Materials and Methods:

Two paddy rice (Oryza Sativa) cultivars IR.579 (indica, long-grain) and Giza 172 (Japonica, Short-grain) were cultivated (June - October, 1978) in Kafr El Sheikh.

The seedlings were transplanted on July, at tellering the equivalent of 50 Kg of N per acre of different straights as well as NP and NPK Viking Ship Complex fertilizers (Norsk Hydro a.s., Oslo, Norway) were to field plots (3 x 3.5m) using the two cultivars in a randomized split plot design with three replicates. At harvesting, straw and grain yields were air dried, divided and weighed. The least significant difference was estimated by the t-test according to Speigel (1972).

The soil used was of the alluvial sodic type with 55% clay, 2% carbonates and a pH of 8.2. The soil had a relatively high ground water table (1 meter from surface). By the end of the growing season and after drying off the fields, the water infiltration rate was measured by the double-ring infiltrometers according to Gaheen and Njos (1978). At the same time soil samples from the rhizosphere were taken. From these samples soil fauna were extracted, counted and differentiated according to Tudros et al. (1965).

Results and Discussion:

The effect of different fertilizer treatments on grain rice yields (table 1) was such that the yield of cv. 579 was generally higher than that of cv. 172. However, with the two varieties the yield was generally, significantly, higher with the NPK than the NP or N treatments. This result suggested that K was a limiting factor for rice production in Egypt. Ammonium sulfate was found to decrease rice grain yield (Helal, 1975). On a similar soil a significant increase in yield of corn (Nafadi and Gohar, 1975 and Faizy, 1979) and seed cotton (Faizy, 1979) were reported with K-fertilizers.

With the two cultivars of rice, the highest yield was obtained with the 21 7 14 grade. Indicating that unlike in cotton where the highest yield was obtained with a fertilizer having an N/K_2O ratio of 1 or less (Faizy, 1979), in paddy rice the most suitable N/K_2O ratio was 1.5 (Ismunadji et al. 1973).

The grain yield as well as the density of soil fauna was higher with urea super granules than ordinary urea (Becham, 1972), indicating that the slow rate of urea granule dissolution was more favorable. Alternatively, the increase in the density with the 23 23 - than the 20 20 - seemed to be due to the high rate of water soluble P of the former than the latter grade.

It was of interest to note that the density of collembola was positively correlated with the grain yield (fig 1). The yield increased hyperbolically with increasing collembola and leveled off at about 70 collembola/500g soil. The density of collembola was similarly related to the dry weight of roots (fig 2). These observations suggested that the density of collembola might be taken as a biological test for soil productivity (Buckle, 1921, and Brauns, 1955). The dry weight of roots of

Table 1: The grain and straw yield as well as the density of total fauna of two rice cultivars as affected by different fertilizer treatments.

	N %	P_2O_5 %	K_2O %	Grain[1] g./sq.m		Straw[2] g./sq.m		Total fauna/500g soil	
				cv.172	cv.579	cv.172	cv.579	cv.172	cv.579
-K	$(NH_4)_2SO_4$	-	-	315.3bc	308.0 c	526.7 f	754.7 d	164.	30.
	Urea	-	-	254.0 c	274.3 c	611.7 e	646.7 e	28.	76.
	Urea granules	-	-	293.3 c	355.7 b	694.7de	851.7 c	74.	99.
	20	20	-	292.3 c	327.7bc	853.3 c	620.7 e	26.	38.
+K	23	23	-	239.7 c	346.3 b	611.7 e	656.7 e	44.	42.
	20	11	11	234.7 c	357.3 b	663.3 e	539.3 f	43.	36.
	15	15	15	237.7 c	375.7ab	715.0de	713.3de	54.	18.
	25	7	7	334.4 b	376.0ab	723.3 d	990.0 b	161.	64.
	16	11	14	345.7 b	390.0ab	589.3fe	691.0de	94.	166.
	21	7	14	409.3ab	454.3 a	1005.0 a	1099.3 a	93.	70.
	L.S.D.			79.3	11.5	64.5	116.2	-	-

Figures followed by same letter are not significantly different at $t_{0.95}$

L.S.D. of 1 and 2 are 95.4 and 90.4, respectively.

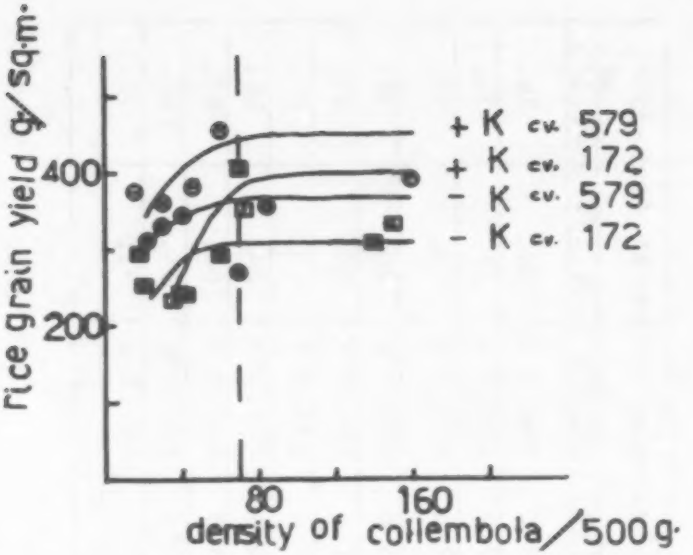


fig. 1. The relationship between the rice grain yield and density of collembola for the two rice cultivars. The dashed vertical line represents the limit of response of collembola to yield increase.

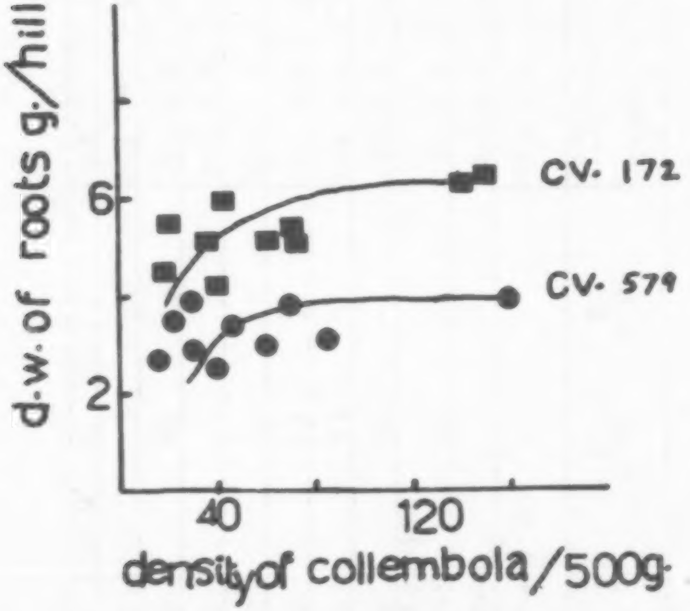


fig. 2. The relationship between dry weight of roots and density of collembola in rhizosphere of two rice cultivars.

the two rice varieties were also hyperbolically related to the density of acarina (fig 3).

The rice grain yield as well as the density of collembola were negatively correlated with the water infiltration rate (fig 4). In contrast to Wilcke (1963), this surprising result might be due to the high salinity of the soil, which might have caused some subsurface cracks upon drying (Russell, 1972).

At a constant N supply (50Kg/acre), K and P were increased (from 14 to 50Kg/acre) with different NPK grades (table 1). The influence of this increase on the density of insect population was such that with cv. 579, the density decreased (fig 5), whereas with cv. 172 the density increased (fig 6). This striking difference suggested that soil insects were not only related to species (von Emdem, 1974) but were also a function of the cultivar. It was therefore tentatively suggested that the insects might have been either feeding on root-parasites or the root itself of cv. 172; whereas with cv. 579 which was found to have a high response to K fertilizers (von Uexkull, 1976). This K might have given the cv. 579 a thicker and harder root cell walls or a low palatability (Mengel, 1976, Ismunadji, 1976, and Trolldenier and Zehler, 1976) and thus rendering it more invulnerable to invasion of parasite and soil insects.

With the different fertilizer treatments, the acarina made up about 10% of the total density of fauna. This percentage was very low when compared to that (45%) reported for the acarina of a bar soil from the same area (Tudros, 1975). This difference might be mainly due to water submergence and the resultant reducing conditions which are usually induced in paddy rice fields.

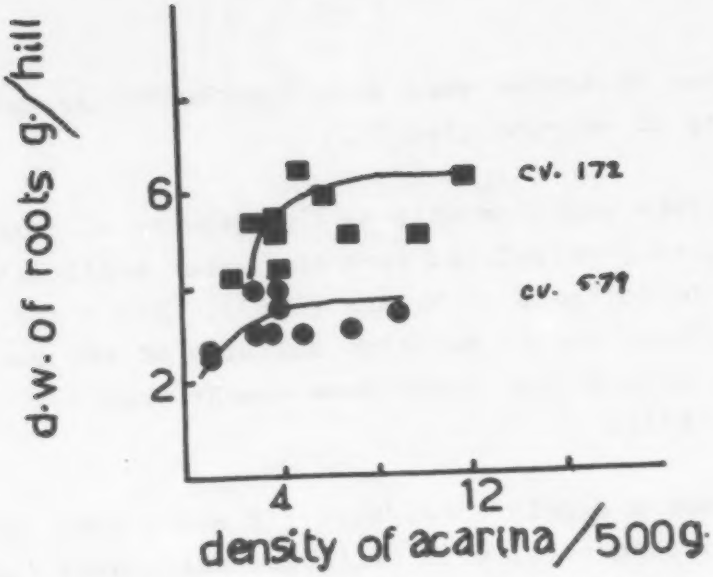
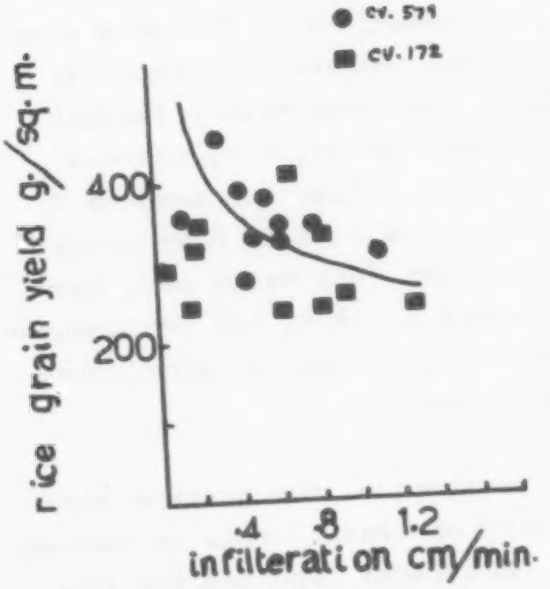


fig. 3. The relationship between dry weight of roots and density of acarina in rhizosphere of two rice cultivars.



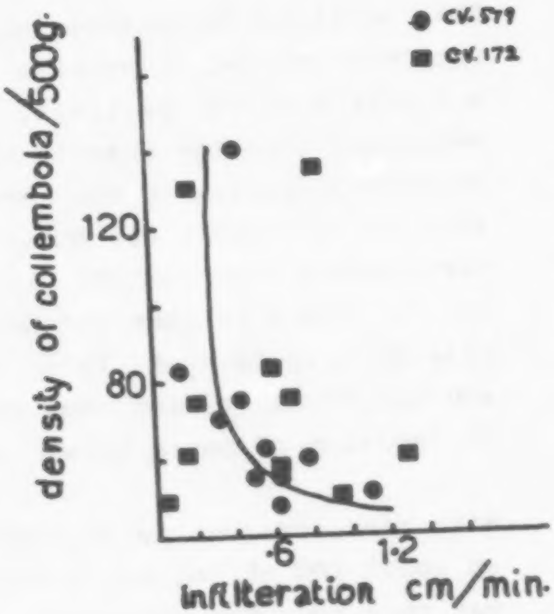


fig. 4a. Relationship between grain yield of two rice cultivars and water infiltration rate.

fig. 4b. Relationship between density of collembola in rhizosphere and water infiltration rate for two rice cultivars.

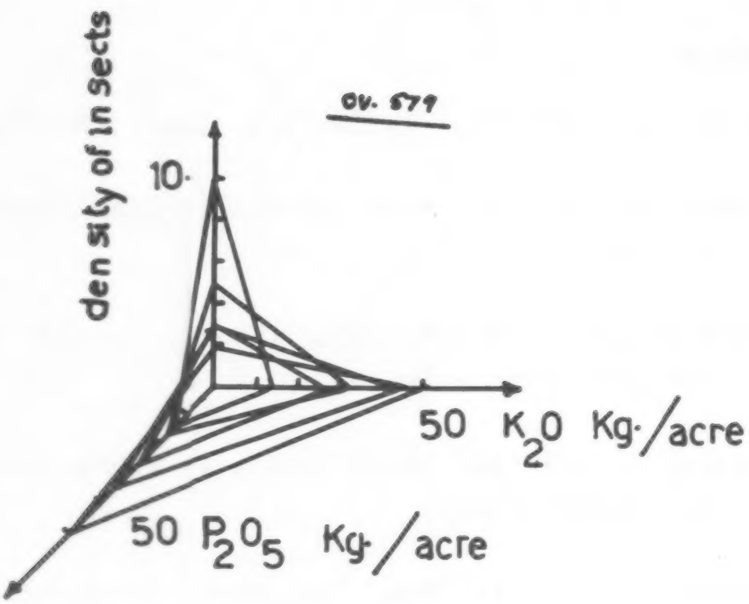


fig. 5. Density of insects per 500g. of rhizosphere soil as affected by variation in K- and P- at a constant N-fertilizers.

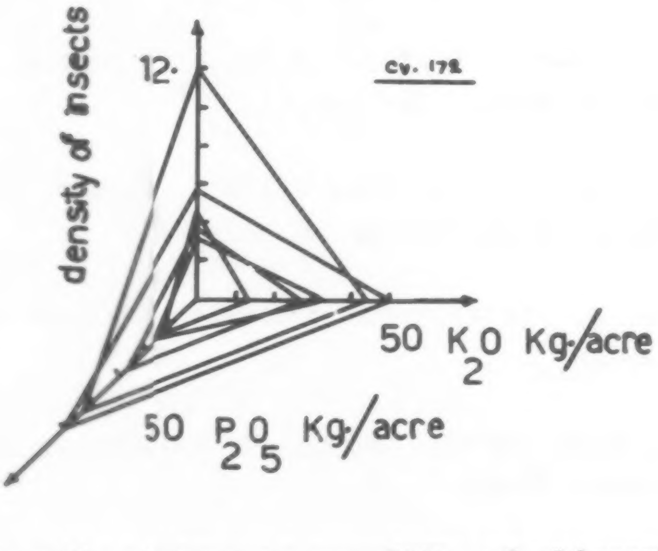


fig. 6. Density of insects per 500g. of rhizosphere soil as affected by variation in K- and P- at a constant N-fertilizers.

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THE ABUNDANCE OF SOIL ANIMALS (MICROARTHROPODA, ENCHYTRAEIDAE, NEMATODA) IN A CROP ROTATION DOMINATED BY LEY AND IN A ROTATION WITH VARIED CROPS

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The effects of different cropping systems on the abundance of soil fauna is studied as a part of the project:
"Ecological systems in arable land" at the Swedish University of Agricultural Sciences.

This is a preliminary report from a soil fauna investigation in an agricultural field trial, located in Ås near Östersund in central Sweden, where a crop rotation dominated by ley (short-term grassland) is compared with a rotation with varied crops. The trial was started in 1955. The experimental plots measure 19.0 m x 6.0 m and are replicated in two blocks. All crops in both rotations are grown every year, so it is possible to study all years in a rotation at the same time.
(See table 1.)
Crop rotation 1 represents a farm with dairy cattle where all crops are used on the farm as forage and large amounts of farmyard manure are produced. Crop rotation 2 represents a farm without cattle where all crops are sold and no farmyard manure is available.

Table 1. Long-term field experiment with different cropping systems at Ås, near Östersund in central Sweden. Soil fauna investigations were carried out in the treatments underlined.

CROP ROTATION 1

Crops	Fertilization kg x ha^{-1} N	P	K	Farmyard manure
Barley undersown with ley mixture	10	35	60	30×10^3
Ley, year 1	90	--	--	--
Ley, year 2	90	15	60	--
Ley, year 3	90	15	60	--
Ley, year 4	90	15	--	30×10^3
Ley, year 5	90	15	40	--
Σ	460	95	220	60×10^3

CROP ROTATION 2

Crops	Fertilization kg x ha^{-1} N	P	K	Farmyard manure
Barley undersown with ley mixture	30	25	60	--
Fallow	30	--	--	--
Autumn-sown rye	50	25	80	--
Peas	15	25	80	--
Potatoes	100	35	200	--
Carrots	75	35	140	--
Σ	300	145	580	--

The soil of the experimental site is a clay loam with about 7 % organic matter. The pH of water extract is about 5.9. In 1966 investigations showed differences in soil physical properties created by the different crop rotations (Håkansson 1968). The mean porosity was significantly higher ($p < 0.05$) in rotation 1 than in rotation 2 when barley undersown with ley mixture was grown (54.4 and 49.9 % by volume respectively). Analyses for organic carbon in 1972 showed a higher level in rotation 1 than in rotation 2 (3.68 and 3.26 % by weight respectively).

The soil fauna samplings were carried out in September 1977. To compare the crop rotations, samples were taken in barley undersown with ley mixture in both rotations. To compare the five year old ley in crop rotation 1 with the succeding barley undersown with ley mixture the five year old ley was also sampled.

The fauna groups studied were:

Microarthropoda: only Collembola and Acari are discussed here. Other arthropod groups were also recorded but their abundance was to low to be measured accurately with the small sample units used. Collembola are classified as one group. Acari have been divided into the suborders Mesostigmata, Prostigmata, Astigmata and Cryptostigmata. Among the Mesostigmata only the cohort Gamasina was found.

Enchytraeidae: this group has not been divided further taxonomically

Nematoda: this group has been divided into ecological feeding groups after Banage (1963), (figure 2).

Sampling for Microarthropoda was made with a cylindrical soil corer with a diameter of 33.5 mm. The sampling depth was 0-10 cm. 20 sample units were taken in each treatment, 10 from each plot. The animals were extracted with a high gradient canister extractor (Macfadyen 1961) further developed at the Mols laboratory in Denmark (Persson & Lohm 1977, Petersen 1978). Sampling for Enchytraeidae was performed with a cylindrical corer of 53 mm diameter. The sampling scheme was the same as for Microarthropoda. The animals were extracted with a modified Baerman funnel method described by O´Connor (1962). Samples for nematodes were taken with a soil borer of 20 mm diameter to a depth of 20 cm. 30 random samples from one plot were pooled. 4 pooled samples were taken in each treatment. The nematodes were extracted according to the method described by Seinhorst (Southey 1970). The microarthropods and enchytraeids were counted under a stereo microscope (5 - 40 X) and arithmetic means, standard errors, ANOVAs and Duncan's tests were computed with BMDP computer programs from UCLA, U.S.A..

The results from the Enchytraeidae and Microarthropoda investigations are shown in figure 1. Generally speaking the different soil animal groups show a tendency of decreasing abundance as follows:

Five year old ley in crop rotation 1. > Barley undersown with ley mixture in crop rotation 1. > Barley undersown with ley mixture in crop rotation 2. The results from the nematode investigation show the same pattern as the Microarthropoda, although the differences are not significant (figure 2). The distribution between the ecological feeding groups is constant with a majority of plant and fungus feeders.

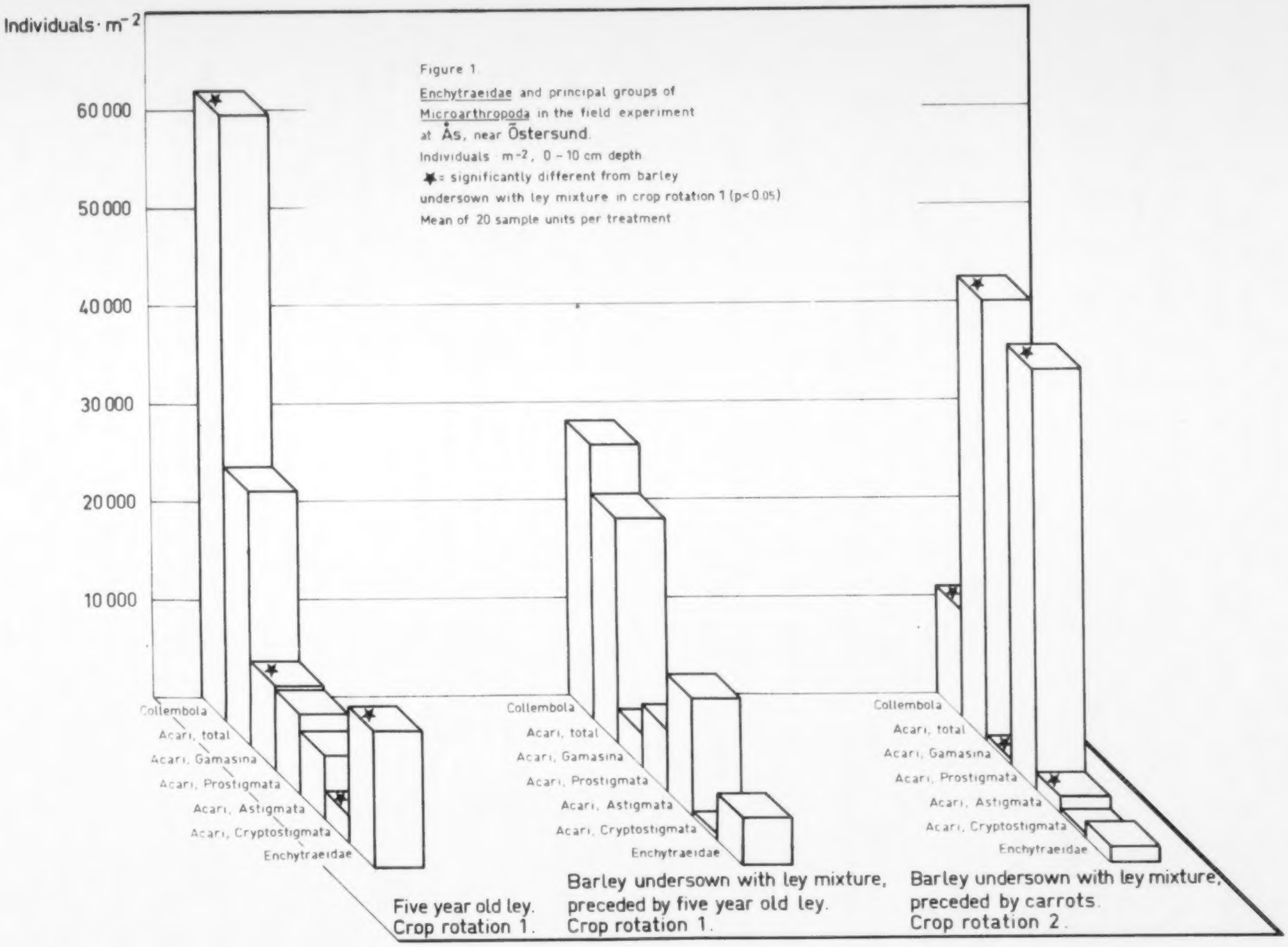

Figure 1.
Enchytraeidae and principal groups of Microarthropoda in the field experiment at Ås, near Östersund.
Individuals m-2, 0 - 10 cm depth
★= significantly different from barley undersown with ley mixture in crop rotation 1 ($p < 0.05$)
Mean of 20 sample units per treatment

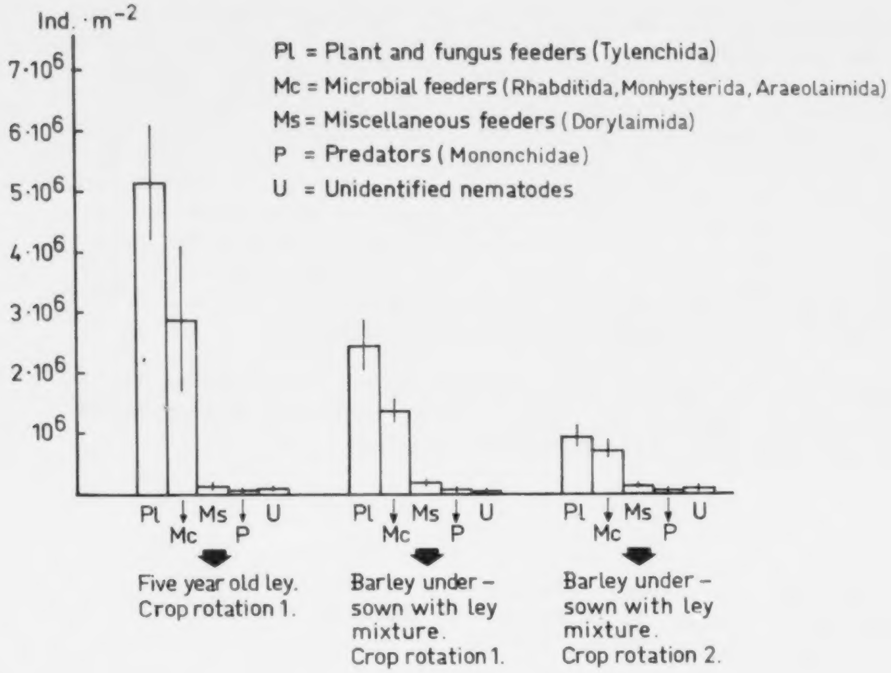

Figure 2.

Nematoda of different ecological feeding groups in the field experiment at Ås near Östersund. Individuals $\cdot m^{-2}$, 0-20 cm depth. Means of 4 pooled samples are shown with their standard errors.

It is not surprising that the old ley has the greatest abundance for most of the groups studied. The soil has not been ploughed for five years, the surface has been constantly covered with vegetation and a great root biomass has developed.

In barley undersown with ley mixture in crop rotation 1 the abundances of Collembola, Gamasina, Cryptostigmata and Enchytraeidae are significantly lower than in the five year old ley by which it is preceded in the rotation. Probably ploughing is the main factor involved. Similar effects of ploughing have been reported from other investigations (Edwards & Lofty 1969, Ryl 1977). Collembola are reported to recolonise rather quickly after ploughing while Gamasina and Cryptostigmata are slower (Sheals 1956) probably due to longer generation time. The Acari group Astigmata shows a higher abundance in barley in rotation 1 than in the other treatments, especially the deutonymph stage, hypopus. The Astigmata seem to have derived advantage from the decaying roots and litter resulting from the ploughing of the ley. The addition of farmyard manure is probably also important, as earlier experiments show (Marshall 1977).

Barley in crop rotation 2 has low abundances for most soil animal groups investigated. The mite group Prostigmata is an obvious exception, with a mean abundance four times higher than in the other treatments. Almost all Prostigmata found here belong to the superfamily Tarsonemoidae, small forms measuring around 0.3 mm or less in body length . These small mites which are fungivores, plant feeders or insect associates seem to have a greater chance to exploit the soil in crop rotation 2 than other, larger forms which might have difficulties because of the low porosity, the changing environment with soil cultivation every year and the less stable humidity and temperature conditions than in crop rotation 1. The scarcity of competitors and predators probably give this group a better chance of survival in this treatment than in the others.

The authors would like to express their gratitude to the staff of the Division of Nematology, Swedish University of Agricultural Sciences for the extraction and analyses of the nematode samples.

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COMPARISON OF MINERAL ELEMENT CYCLING UNDER TILL AND NO-TILL PRACTICES: AN EXPERIMENTAL APPROACH TO AGROECOSYSTEMS ANALYSIS

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The soil fauna of cultivated agronomic systems is notoriously improverished, supporting low populations of soil arthropods in comparison with uncultivated, natural forest or grassland ecosystems (Edwards and Lofty, 1969; 1973). Tillage practices can cause appreciable disruption of soil structure and biological communities (Allison, 1973). Cultivated soils also show large decreases in organic matter compared to untilled soils (Brady, 1974). Typical modern agricultural techniques replace naturally occurring soil structure and function with a virtually sterile medium for culture of a single crop species at high density. It is ironic that much of our knowledge of physical and chemical properties of soils, and even microbial properties, is derived from studies of such highly modified systems. Knowledge of soil zoology is more nearly based upon studies of undisturbed systems.

In the past decade several developments have converged to promote an increased interest in soil zoology of agronomic systems. One development is the utilization of an ecosystem viewpoint, emphasizing holistic approaches (Harper, 1974). A major catalyst has been the use of nutrient cycling as an integrating paradigm for evaluating whole ecosystems performance and response to disturbance (Bormann and Likens, 1967). The interactions of major ecosystems processes (primary production, consumption, decomposition and abiotic processes) have been evaluated using nutrient flows, in a variety of natural or managed ecosystems, as evident by several papers at this symposium. Another development has been the increasing adaption of minimum tillage or no-tillage agronomic practices (Pereira, 1975). Whatever their other benefits, reduced tillage practices result in richer soil biota, including invertebrates (Edwards and Lofty, 1973; House, 1979). Increased awareness of the importance of mycorrhizal associations for some crop systems has suggested that tillage practices might be modified. Increasing costs of energy for cultivation and chemical amendment, and awareness of the need to reduce sediment and chemical pollution of waterways, are additional considerations leading to reduced cultivation practices. In any event, reducing tillage allows soil biological components and processes to operate in a manner similarly to those in undisturbed ecosystems.

In this paper we give an overview of a research project which is attempting to integrate the approaches of agronomy and ecosystem ecology. We are attempting to apply methodologies and approches of ecosystem study, in particular nutrient cycling, as a means of evaluating performance of agronomic systems. Specifically, we are comparing structure, function and nutrient dynamics in a set of no-tillage and conventional plots.

No-tillage or minimum tillage farming excludes or reduces plowing and smoothing the soil prior to planting (Phillips and Young, 1973). Seeds are planted in the residue from the previous crop. The only disturbance to the soil is the narrow cut for the seed furrow. Special planting equipment is used for this operation. Conventional tillage usually entails six or more trips across the field (plowing, disking, planting, cultivating at least once, herbiciding and harvesting). No-tillage requires only one trip each for planting, herbiciding and harvesting, and thus is energetically more efficient than conventional tillage. Important benefits from no-tillage practices are conservation of soil and water resources. Also, as described above, perturbation of soil structure is substantially decreased. However, there are some disadvantages to no-tillage: Weed problems can be severe, although companion planting can reduce weed growth (Phillips and Young, 1973). Some studies (Musick and Petty, 1974) have shown increased insect problems in no-tillage. Still, no-tillage farming is increasingly popular.

The research project described here is currently in its second year of development, and is the joint effort of several ecologists at the University of Georgia. Results given here are fragmentary and preliminary, but representative. Data are presented on plant growth, decomposition, soil microarthropods and nutrient leaching. Other information on canopy consumers, soil, fertility, microbial processes, soil microarthropods and chemical transformations is not yet ready for reporting.

The foundation for our experimental approach is the general hypothesis that no-tillage practice leads to nutrient and energy conservation. Biotic and abiotic components of soil, left undisturbed, are organized into a well-defined structure, with the result that nutrient cycling reduces loss of nutrients from the system. This paradigm is supported by watershed studies (Bormann et al. 1974; Waide and Swank, 1976) showing that in forested areas (highly structured systems) internal cycling greatly exceeds throughput. Plowing once or twice yearly is a major perturbation which destroys the soil system's structure and function, and recycling of nutrients becomes minimal. Conventionally tilled farm land is in essence kept in a very early successional or immature state by man-induced subsidies. No-tillage farming allows soil structure to develop. Biotic components remain relatively undisturbed and therefore the no-tillage system should have more of its recycling processes intact.

EXPERIMENTAL DESIGN AND METHODS

Horseshoe Bend is a 40-acre tract of land located in Clarke County, Georgia. The area is an alluvial flood plain adjacent to the Oconee River (Barrett, 1968). The crop system we are using consists of eight ¼ acre plots, bordered on two sides by an old-field. As of May, 1978, the area which is now the crop system was in old-field vegetation, not having been cultivated for 12 years. In May, the area was cleared of vegetation to ground level. Eight experimental plots, randomly selected, received either conventional plowing or no-tillage treatment. Following standard fertilizer applications, atrazine was used as a pre-emergence herbicide. Grain sorghum was planted using a no-till planter. In the fall of 1978, both till and no-till plots were planted in winter rye which was consequently mowed and chopped in the spring of 1979. Sorghum was again planted. Through-out, we have used standard cultural recommendations for sorghum in the Georgia piedmont.

Both above and below ground sorghum biomass was sampled at two week intervals using three 1-m^2 quadrats randomly located in each of the eight plots. Plant material was oven-dried to constant weight for biomass determination, ground, and subsampled for nutrient measurements utilizing a plasma emission spectrograph. Grain production was evaluated from similar 1-m^2 collections made at the time of harvest.

Litterbag techniques were used to measure rates of decomposition (Crossley and Hoglund, 1972; Edwards and Heath, 1963). Litterbags containing weighed crop residue were randomly distributed over the soil surface of each treatment soon after planting. Five bags per plot were randomly collected at approximately two week intervals. The residue was oven-dried to constant weight in order to calculate loss of material, ground and retained for nutrient analysis.

Soil microarthropods were sampled by extracting them from soil cores (5 cm dia. by 5 cm deep) on a modified Tullgren apparatus (Merchant and Crossley, 1970). Ten random cores were taken from each plot at two week intervals. The soil microarthropods were also sampled prior to plowing and planting. Gross counts by major taxonomic groups made on these samples are now available, and more detailed analysis of the faunal structure is continuing.

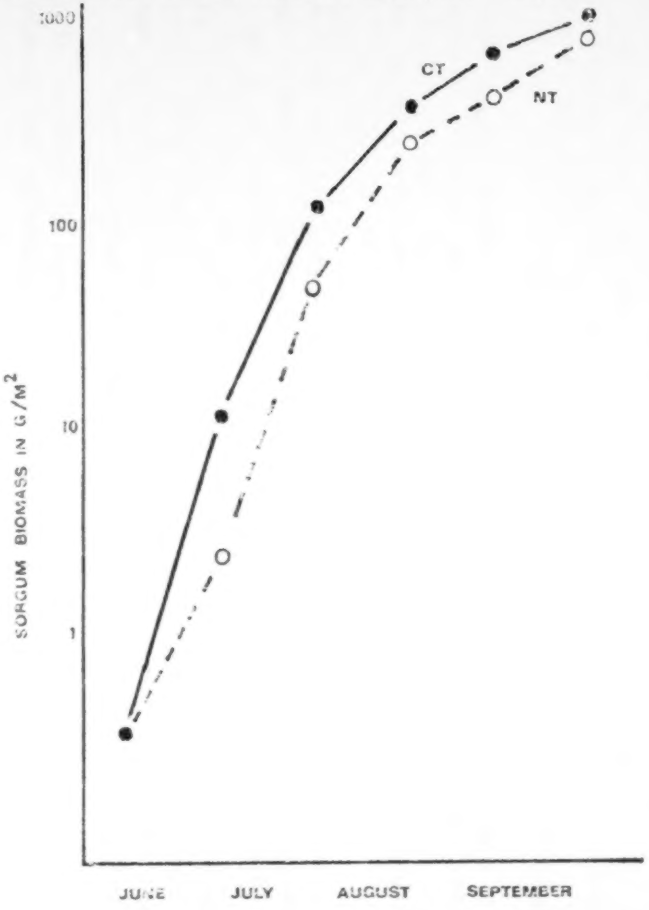
Because the experimental area is flat with minimal or no surface run-off, the major loss of nutrients is through the downward movement of ground water. Porous cup lysimeters (Soil Moisture Corp.) were used to measure the concentration of nutrients (NH_4, NO_3, P, K, Na) at a depth of 50 cm. This measurement is considered to represent loss concentration, since the area of nutrient uptake by sorghum is generally above 50 cm. The lysimeters were sampled approximately every two weeks. The ground water was analyzed for ammonia and nitrate nitrogen using colorimetric techniques. Cation and phosphorus determinations are being made with a plasma emission spectrophotometer.

RESULTS AND DISCUSSION

The results of these studies obtained so far confirm the advantages of no-till practices over conventional tillage. Only results from the summer of 1978 are available, and these results cover but a few of the process-level measurements.

Primary production in no-till and conventionally tillage plots, as revealed from harvests of sorghum, produced nearly identical plant biomasses by the end of the growing season. Figure 1 shows that sorghum

FIGURE 1. Above-ground biomass of grain sorghum in conventionally-tilled (CT) and no-tillage (NT) experimental plots, Horseshoe Bend Experimental Area, Athens, Georgia. 1978.



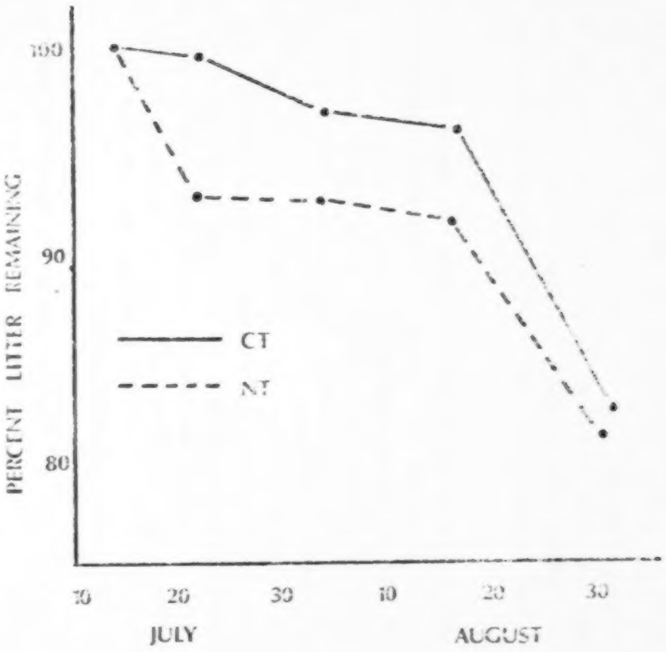


FIGURE 2. Retention of dry weight by litter confined in small-mesh bags placed in conventionally-tilled (CT) and no-tillage (NT) experimental plots, Summer, 1978.

growth in no-till plots initially lagged behind growth in cultivated plots. Leaf formation and heading time also lagged behind in the no-till plots. A significant factor may have been the slower root development in no-till plots, which itself may have been influenced by an early-season drought. As Figure 1 shows, at the end of summer sorghum biomasses were similar in conventional and no-tillage systems. Biomass of weeds was higher in the no-till plots in the first week's samples, but thereafter weed biomasses were similar for the two treatments.

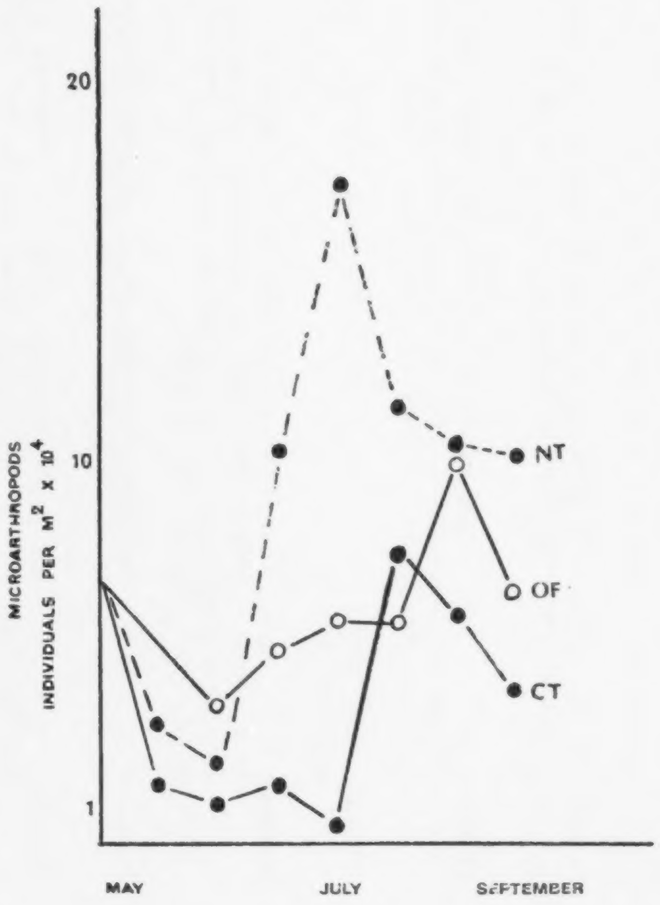
Weight loss by plant residue, as measured by litterbag techniques, is illustrated in Figure 2. In each treatment weight loss was slow, but increased abruptly in late summer. Litter confined in bags in the no-till plots lost weight more rapidly than that in the conventional tillage treatment, but final percentages of litter remaining were similar (Figure 2). The pattern of weight loss and decomposition of surface litter during the winter season may be of greater significance than results for the summer growing season. Total decomposition might be expected to proceed more rapidly under cultivation, since surface litter becomes incorporated into the mineral soil. However, the ameliorating effects of surface litter on abiotic microclimatic factors in no-till systems may negate this influence of cultivation, at least in some years.

Populations of soil microarthropods in conventional, no-till and old-field plots showed an initial decline followed by an increase later in the summer (Figure 3). Very low values obtained for microarthropod populations in cultivated plots during June or July (about 1000 per m^2), but these numbers increased dramatically following July rains (Figure 3). A complete analysis of soil microarthropod responses to tillage practices in these plots has been developed (Weems, in preparation) and will be presented elsewhere. Similarly, pitfall trapping has been used to compare populations of surface-dwelling macroarthropods in these tillage comparisons (Blumberg, 1980).

While we are attempting to develop input-output budgets for several major nutrients, we are placing particular emphasis on nitrogen fluxes and transformations. Reid et al. (1969) suggested that nitrogen regimes are principally functions of immobilization and remineralization rates, processes largely mediated by microbial activities. While large gaseous fluxes of nitrogen occur in soil systems, leaching losses may be appreciable as well, particularly in the humid southeastern United States (Nelson and Uhland, 1955). Figure 4 shows nitrate nitrogen concentrations in lysimeter collections at 50 cm depth in conventional and no-till plots. During the last half of the summer, nitrate concentrations in groundwater were significantly higher in the conventionally tilled plots. These data suggest that no-tillage practices retard nitrate loss via leaching. Further evaluation must be based on gaseous transformations as well as leaching losses.

Figures 1 - 4 are illustrative of the types of research data being collected in this field experiment. We emphasize the phenomena

FIGURE 3. Total microarthropods in top 5 cm of conventionally-tilled (CT), no-tillage (NT) and old-field (OF) soils, Horseshoe Bend Experimental Area, Summer, 1978.



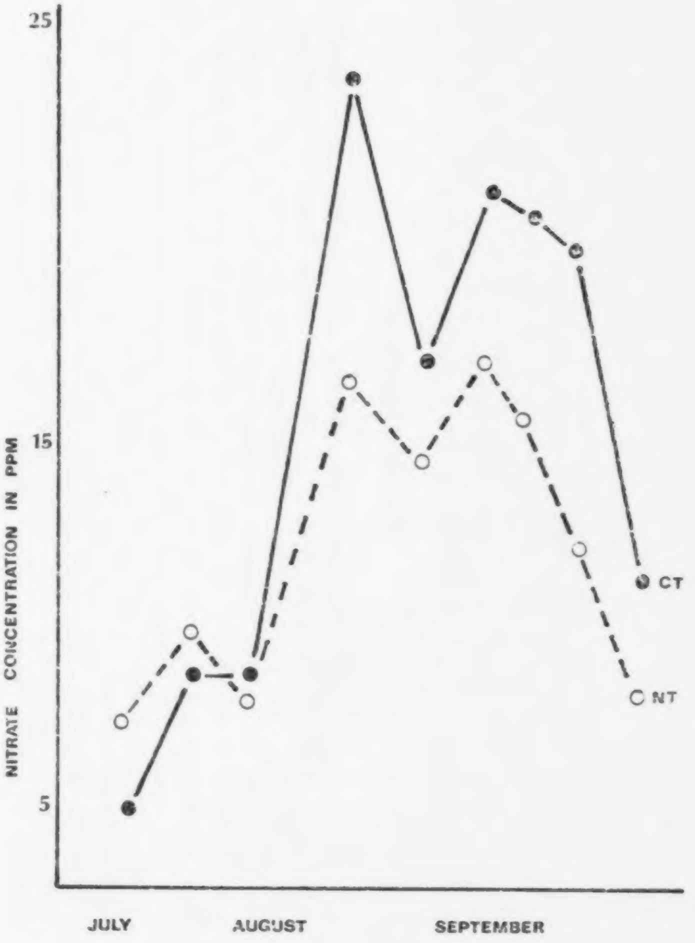


FIGURE 4. Nitrate-nitrogen concentrations in groundwater collections from porous cup lysimeters at depths of 50 cm in soils of conventionally-tilled (CT) and no-tillage (NT) plots, Summer, 1978.

pertaining to the soil constitute the major differences between the experimental systems. A generalized overview considers nutrient inputs and outputs in contrast with internal nutrient dynamics in these systems. The principal nutrient input for both systems is the fertilizer subsidy. Harvest of crops is a major nutrient output, but so are leaching and (for nitrogen) gaseous losses. The regulation of the latter nutrient export is a function of the soil system and is mediated by soil biological communities. It appears from our results to date, that the more intact soils of no-tillage agronomic systems should prove to be more conservative of nutrients.

ACKNOWLEDGEMENTS

We are reporting the team efforts of a number of scientists, students and others interested in the changing face of American agriculture. We gratefully acknowledge the contributions of all of them, especially Drs. Eugene P. Odum and Robert L. Todd, Institute of Ecology, University of Georgia. We are especially grateful to Dr. A. Kumura, Mr. Greg Hoyt, Ms. Anne Kimber, Ms. Georgianna May, and Mr. Danforth Weems, for the use of their previously unpublished data. Support for this research was provided by the Department of Entomology and the Institute of Ecology, University of Georgia. Research on populations and activities of soil arthropods was supported by a contract (DE-A509-76EV00641) between the Department of Energy and the University of Georgia (D. A. Crossley, Jr.).

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F. GOULD: Did you monitor weeds?

B.R. STINNER: Yes, we did. Biomass of weeds was higher in no-till plots in the first samples we took. By the end of the summer, the weed biomass in conventional tillage was just as high as in no-tillage.

E. WALDORF: Was insecticide applied in your conventional tillage? If not, how does this compare with agricultural practice?

B.R. STINNER: No, we didn't apply any insecticide. This would not be unusual for grain sorghum in our area.

C.A. EDWARDS: We have also found fewer attacks by stemborers in no-till systems.

The slow initial growth you reported was a normal response. We have always found slower initial root growth under no-till but later in the season root growth catches up and overtakes that in ploughed soil.

I am not so sure about the nutrient situation. In England we often have to add extra nitrogen to no-till crops and less of other nutrients.

EFFECT OF MEADOW MANAGEMENT ON SOIL PREDATORS

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The thesis of this contribution is that meadow management is usually followed by a decrease, in the abundance of invertebrates, predators being most heavily reduced as compared with other trophic groups. This refers both to the predators occurring aboveground and to the predators inhabiting soil and soil surface.

In unutilized ecosystems, or in those extensively utilized, the abundance of invertebrate animals is closely correlated with available food supply. There is a relationship between the amount of organic matter dying over the year and the biomass of saprophages [fig. 1]. There is also a relationship between the biomass of saprophages and the biomass of predators [fig. 2]. The regression describing this relationship has been calculated from data on 12 ecosystems [Kajak, 1977]. There is also a relationship between the rate of dead matter input and the predator biomass in an ecosystem, although the biomass of predators in a given area is extremely small [10^{-4}], as compared with the amount of dead organic matter. Nevertheless, the abundance of predators depends on the amount of this matter. Both the average biomass of predators and the average biomass of saprophages are a function of dead matter input.

A regression of the average annual invertebrate biomass on the annual input of dead plant material was calculated. The functions were verified by the analysis of variance on the basis of F statistics. The value of F obtained from the empirical data is higher than the theoretical F at the level 0.01 for all the functions [fig. 1 and 2].

In intensively utilized ecosystems these relationships are disturbed. The number of predators is extremely small in relation to food supply in such ecosystems. When analysing this problem, such factors as numbers, biomass, and lobomotory activity of predators were considered. Author's own observations were used and the literature data.

I am going to start with a very actual problem, analysed by a group of research workers of the Institute of Ecology, Poland, for some years, namely with the problem of the effect of mineral fertilizers on a meadow ecosystem.

The meadow was fertilized only with main macroelements - NPK, at a rate of 680 kg · ha^{-2}. As a result,

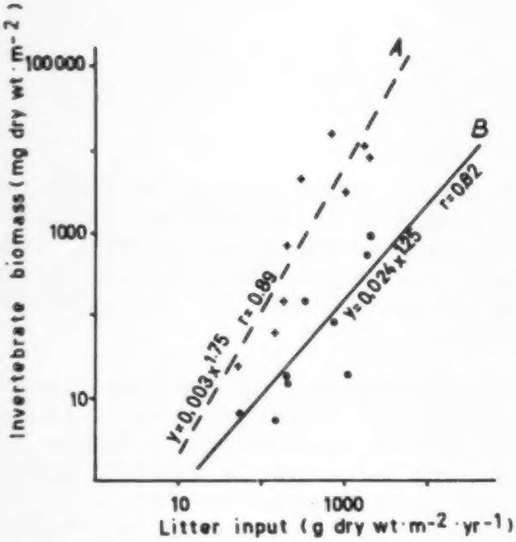

Fig.1. Relationship between litter input and saprophage (+,A) or predator (•,B) biomass.

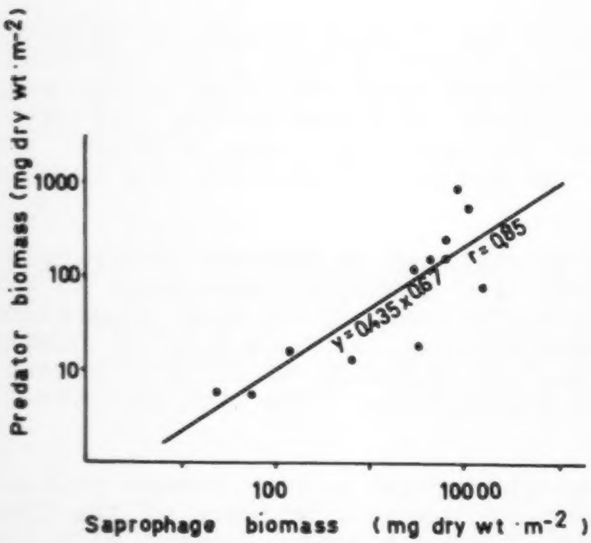

Fig.2. Relationship between saprophage and predator biomass.

the soil was acidified [PH KCl 5-5.6 in the control plots, while 4.5-4.8 in the fertilized plots]. There were some losses in the exchangeable Ca and Mg and decrease in sorption capacity in the soil [Czerwiński an Pracz 1978]. At the same time some changes occurred in the living part of the ecosystem. The yield increased, plant species and their chemical composition being changed. This was followed by an increase in the number of phytophagous insects living on green plant parts. The biomass of soil fauna decreased for all the trophic levels. The biomass of predators, however, dropped most, by more than 60% in the third year of fertilizer application, while the biomass of saprophages and phytophages dropped by about 20%. Thus the proportion of predators decreased in relation to the total biomass of invertebrates. [Tab. 1].

Tab. 1
Effect of fertilizing on soil meso - and macrofauna

Trophic groups	Mean biomass [g. d.wt. · m^{-2}]	
	Control plots	Fertilized plots
Predators	0.57	0.19
Herbivores	2.05	1.49
Saprophages	26.85	23.09
Total	29.47	24.77
Predators/Total in %	2.00	1.00

after Andrzejewska, 1976, Makulec, 1976; Nowak 1976; Olechowicz 1976; Pętal, 1976; Wasilewska, 1976; Żyromska-Rudzka, 1976, Kajak 1977.

However the total number of predators was not affected, only the proportion of small size animals increased in the carnivore level. [Tab. 2].
The number of such small arthropods as Staphylinidae increased, while the number of larger predators such as Carabidae and Chilopoda decreased. At the same time, the average body weight of an individual increased in the group of predators of small size, and dropped in the group of large ones. [Tab. 3].

In the community of spiders, which are animals of intermediate size as compared with the groups earlier discussed, no significant changes in the density were observed [Tab. 2], only the proportion of particular species was changed. In the fertilized plots the heaviest species declined, [*Tarantula pulverulenta* /Cl/, *Trochosa ruricola* Koch, *Pardosa palustris* /L/], while an increase in number was observed in the species of small body size, [*Erigona atra* Bl., *E. dentipalpis* /Wid./, *Centomerita bicolor* /Bl.] [Tab. 4].

Tab. 2
Effect of fertilizing on density and biomass of predatory arthropods

Small animals		Number of ind · m^{-2}		mg d wt · m^{-2}	
		Control plots	Fertilized plots	Control plots	Fertilized plots
Staphylinidae im.	1973	110.5	142.2	26.5	48.3
	1974	69.7	84.6	20.1	39.9
Staphylinidae larvae	1973	96.0	139.4	8.3	14.4
	1974	54.2	58.1	3.2	6.8
Large animals					
Araneae	1973	37.7	73.7	106.7	71.5
	1974	35.4	28.8	34.0	19.7
Chilopoda	1973	61.3	10.3	25.1	4.3
	1974	86.5	68.8	179.2	79.5
Carabidae im.	1973	3.01	1.71	53.3	22.9
	1974	5.46	5.58	88.5	13.4
Total	1973	309.4	367.3	220.0	161.4
	1974	251.3	247.9	325.0	159.3

Tab. 3 Mean individual weight

Small animals	Year	mg d wt		Method
		Control plots	Fertilized plots	
Staphylinidae im.	1973	0,24	0,34	soil cores
	1974	0,33	0,37	
Carabidae larvae	1973	0,086	0,10	soil cores
Large animals				
Areneae	1973	2,83	0,97	quadrate method
	1974	2,00	0,79	
Carabidae	1974	17,7	13,4	soil cores
	1975	35,1	24,2	pitfall traps

Tab. 4 Effect of fertilizing on density of dominant spider species

Increasing body weight	Mean number of individuals . m^{-2}		Mean individual weight mg d. wt
	Control	Fertilized	
Trochosa ruricola	0,45	0,0	73,6
Tarentula pulverulenta	0,47	0,22	16,0
Pardosa palustris	7,67	[illegible],1	4,[illegible]
Pachygnatha degeeri	6,00	[illegible],77	2,1
Centromerita bicolor	2,41	2,55	1,0
Erigone dentipalpis	0,22	1,00	0,71
Erigone atra	0,0	1,50	0,26

The species of intermediate size were subject to smallest changes [*Pachygnatha degeeri* Sund].

Therefore, in treated plots two processes occur at the same time - changes in the body size and in numbers. [Tab. 2, Tab. 3]. In the group of large animals there was a decrease in the average body weight and in numbers, while in the group of small predators an opposite situation was observed. Mean density of predators is similar in treated and untreated areas. [Tab. 2].

A decrease in the body size implies that animals with a higher metabolic rate generally also with a shorter life cycle became more important. As a result, the biomass turnover increased. Also the diet of predators must be shifted towards smaller prey. The decrease in the proportion of predators as such is one of the mechanisms of speeding up the rate of matter cycling [Jakubczyk, Kajak 1977]; a decrease in the size of individuals must have similar consequences.

An accelerated matter cycling can compensate for losses in the nutrients leached from the ecosystem because of increasing acidification, or removed from the ecosystem with increasing yield and not restored because only a limited number of nutrients is supplied with fertilizers. A similar tendency to a diminishing of the body size of animals, as observed in fertilized meadows is also characteristic of crop fields, as compared with natural and semi - natural ecosystems.

The changes in the biomass and species composition of predators in the fertilized plots were associated with a decrease in their mobility. Less animals were caught by pitfall traps. As far as the number of predators did not drop we can assume that the difference in the number of individuals trapped is a result of decreased locomotory activity of arthropods. [Tab. 2 and 5].

Tab. 5
Effect of fertilizing on locomotory activity of predatory arthropods.

	Number of ind per trap • $24h^{-1}$	
	Control plots	Fertilized plots
Araneae	4.77 ± 0.40	3.16 ± 0.18
Formicidae	1.19 ± 0.14	1.20 ± 0.11
Carabidae	0.81 ± 0.07	0.35 ± 0.06

after Kajak, 1977

Similar methods as applied in the analysis of the effect of mineral fertilizing were used to examine the effect of organic fertilizers in the form of sheep manure on an ecosystem. This treatment was followed by a complete change in the vegetation composition and by a raise in yield, as it is the case when mineral fertilizers are applied. The basic difference is that the input of organic fertilizers was followed by an increase in the biomass of soil fauna, including phytophages and saprophages. The biomass of predators, instead, dropped, though not so markedly, as after the application of mineral fertilizers /by about 20%/ /Tab. 6/. The proportion of predators to the total biomass of soil fauna decreased considerably, as it was one-fifth of that in unfertilized plots. The size of animals did not diminish , however.

The analysis of the effect of grazing on predators will be based on data from American prairies. These were long-term studies, thus it is possible to follow long-term effects of enclosing large areas to exclude them from grazing. Many ecosystem components were analysed there, from which only soil fauna will be discussed here. Andrews et al. /1974/ estimated energy flow through short grass prairie ecosystem in the Colorado state. There was compared, among others, respiratory energy loss of three consumer levels in heavily grazed /1 steer/4.8 ha for 180 days/ and ungrazed areas.

Grazing was followed by a decrease in the energy used for respiration by invertebrate animals. And again predators were more affected than other trophic groups. The energy flow through the trophic level of predators dropped almost by half in the grazed prairie, while the amount of energy used by phytophages and saprophages decreased by only a little more than 20% /Tab. 7 A/.

A similar conclusion can be drawn from the studies conducted in prairies of different types /Lewis 1971/. The average biomass of predators in different prairies was higher for ungrazed sites, although, for example, phytophages showed an opposite tendency / Tab.7 B/.

A negative effect of mowing on the number of predators is convincingly illustrated by Southwood and Emden /1967/. According to these authors, phytophagous species tended to be more abundant in the cut grass land while both predatory and saprophagous species are in the most cases reduced in numbers. They have also shown that mowing is followed by a decrease in the proportion of predatory species in groups of animals with large food spectrum such as Acarina, Coleoptera, and Heteroptera /Tab. 8/.

Tab. 6
Effect of manuring by penning sheep on soil meso- and macrofauna.

Trophic group	Mean biomass / g d wt • m^{-2} /	
	Control	Year after manuring
Predators	0.15	0.12
Herbivores	0.28	0.92
Saprophages	4.50	20.60
Total	4.93	21.64
Predators/ Total in %	3.0	0.6

after Delchev, Kajak 1974, Pętal 1974, Wasilewska 1974, Nowak 1975

Tab. 7
Effect of grazing by cattle on activity and biomass of belowground invertebrates.

	Respiration kcal • m^{-2} per 180 days		
	Ungrazed	Heavily grazed	Ungrazed/ Heavily grazed
Herbivores	22.8	17.4	1.31
Saprophages	16.2	12.5	1.30
Carnivores	3.9	2.1	1.86

after Andrews et al. 1974

	$\bar{B}$ ungrazed/ $\bar{B}$ grazed	
	1970	1972
Herbivores	0.8	0.3
Carnivores	1.7	1.9

after Lewis 1971, McDaniel 1971, Grassland Biome Data Bank 1972

Tab. 8
Per cent of predators in total number of individuals

	cut meadow	uncut meadow
Acarina	19.0	32.0
Coleoptera	8.4	20.0
Heteroptera	17.0	22.0

after Southwood, Emden 1967

Summing up, it may be concluded that meadow management is usually followed by a decrease in the proportion of predators in the ecosystem, and by a reduction in the biomass of predators. Their biomass is reduced even in the case when the treatments applied cause an increase in plant biomass and in the potential food resources /e.g. organic fertilizers/. The animals analysed above are polyphagous predators with a relatively long life cycle. Stenophagous predators /e.g. parasites/ were not analysed here, it is even possible that their activity can compensate to some extent for the deficiency of polyphagous predators. The data available seem to indicate, however, that the reduction of predators affects the functioning of one of the mechanisms of number regulation. Another important consequence is the acceleration of decomposition rate as it seems that soil predators inhibit the rate of these processes /Kajak and Jakubczyk 1976, 1977/.

So far pest outbreaks in meadows have been rare as compared with other ecosystems such as forests and crop fields. It seems, however, that the intensification of agricultural treaments enhances pest outbreaks also in meadows.

One of the characteristic features of grasslands is the retention of organic matter in soil humus decomposition processes being generally less rapid than production. As a result of the intensification of management these processes seem to be shifted towards a higher decomposition rate, this making grasslands similar to crop fields.

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QUESTIONS and COMMENTS

M.S. TADROS: What kind of traps were used in this investigation for determining soil fauna activity?

A.J. SZUJECKI: I feel I am unable to answer questions since it is not my work.

S.B. HILL: Did Dr. Kajak examine the influence of time of application of the various management practices on soil fauna. My experience is that timing is critical with respect to both beneficial (intended) and harmful (unintended) effects.

A.J. SZUJECKI: I cannot answer for Dr. Kajak but you are quite right; it is important.

INFLUENCE OF AGRICULTURE ON THE OUTBREAK OF WHITE GRUBS IN INDIA

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INTRODUCTION

Every farmer in India is aware of white grubs but seldom thinks they would cause injury to his crops. The danger is realized only when the crops suddenly start wilting. Such plants are easy to pull up and a white grub can often be scooped up from the soil under the plant. The farmer then thinks that all white grubs are his enemies, although a small percentage of this large group of scarabaeids are phytophagous and the rest are either coprophagous dung feeders or litter inhabitants. Thus the farmers are often hesitant to apply compost and farmyard manure in which many white grubs live, because they think that the white grub problem in the cultivated field is introduced with farmyard manures. Not many realize that the white grubs develop into the beetles that swarm in dusk after the premonsoon showers.

The white grub problem is world-wide, mostly in lawns, turf and grasslands, but in India extensive damage is caused to cultivated crops in addition to lawns and turf. White grub damage to cultivated crops reported from outside India is mostly on sugarcane (Mungomery, 1948; Mautia, 1935; Wolcott, 1935; Jepson, 1956). In India, no crop is free from the ravages of white grubs, except under puddled conditions (Veeresh, 1977).

The seriousness of the problem of white grubs to cultivated crops was not realized until 1956, when a serious outbreak of white grub was reported on sugarcane in Dalmianagar, Bihar (Anonymous, 1956) although early records of white grub damage to crops in India were available (Sharp, 1903; Fletcher, 1919; Beeson, 1919; Anstead, 1919; Isac, 1919; Stebbing, 1899). If the number of publications on white grubs in India is any indication to the magnitude of the problem now and before two decades, certainly the problem has increased in the last two decades. Before 1960 there were only twelve publications on this subject compared to more than two hundred references available now. Realizing the importance of white grups in Indian Agriculture, the Indian Council of Agricultural Research constituted a committee of experts in 1974 to consider the problem and to suggest corrective measures (Anonymous, 1974). Large scale campaigns against white grubs have been launched in the States of Karnataka (Veeresh, 1974), Maharashtra (Raodeo et al., 1976) and Rajastan (Yadava et al., 1978). The ICAR Scientific Panel of Entomology and Nematology has suggested an All India Coordinated Research Project on white grubs, to be taken up in the sixth five year plan.

Perhaps for the first time a single pest has drawn the attention of the whole country. So far there has been no single effective solution for the problem of white grubs in this country and every year damage by the pest increases. An attempt was made to assess the factors responsible for the sudden increase in the white grub incidence. With the evidence available a change in agricultural practices seems to have a major influence favouring the outbreak of this otherwise ubiquitous insect, in the last two decades when the practices of traditional agriculture gradually gave way to modernization.

METHODS

Data has been collected for over twelve years on the incidence of white grubs under different agroclimatic conditions in India both by personal visits and through communication. Response to a quarterly white grub newsletter, issued from the Department of Entomology, University of Agricultural Sciences, Bangalore since 1974, provides information needed to assess the causes for the outbreak of white grubs in this country. Observations were made on major species of white grubs occurring in different agroclimatic conditions, like coastal belts, heavy rainfall plantation districts of western ghats, peninsular India, Northern plains and upper Simla Hills. And also the relation of outbreaks to temperature, moisture, humidity, rainfall, soil types, food preferences, natural enemies and cultivation practices were studied.

One species under each agroclimatic zone was selected for observation. They include *Leucopholis coneophora* Bl. (coastal belt and low lying areas of western ghat slopes), *Holotrichia nilgiria* Arrow (heavy rainfall plantation districts of western ghats), *Holotrichia serrata* F. (Deccan plateau), *Holotrichia consanguinea* Bl. (Northern plains) and *Holotrichia* sp. (upper Simla Hills). The observations were recorded under the following four categories:

1. ADULT: emergence, mating, food preference, flight range, and egg laying
2. LARVA: food habit, migration, effect of moisture
3. PUPA
4. NATURAL ENEMIES OF WHITE GRUBS

At a site selected at Mahadeswarapura, Mandya District, about 130 kilometers from Bangalore, observations were made for the pest outbreak, in relation to changed pattern of agriculture in an area of over 200 hectares, where there was no incidence of the pest before irrigation facilities were created after which the cropping pattern was changed.

RESULTS

ADULT

Emergence

Leucopholis coneophora emerged only after the heavy rains for 3-4 weeks of monsoon in the laterite soils of western ghat slopes and coastal region. *Holotrichia nilgiria* emerged twice a year, although it has an annual life cycle; the first was in April-May after the pre-monsoonshowers and the second time was during post-monsoon period in October-November when there was rain after several days of sunshine. *Holotrichia serrata* emerged immediately after the premonsoon rains in March-April in South India and up to early July in Northern plains depending on the occurrence of rain. *H. consanguinea* found emerging in June-July, when the premonsoon rains occurred, as it confined to the plains of Northern India. All the species emerged in dusk around 1930 hrs except *L. coneophora* which emerged an hour early in cloudy rainy weather. Other species were not active during rainy windy days.

Mating

Mating occurred above ground on host plants or on some trees in all the species except *L. coneophora* which mated on the ground immediately after emergence and went back to the soil after some time. Other species remained active on clear nights till dawn and fed on preferred hosts.

Food Preference

Adults of *L. coneophora* did not feed on any plant nor were they found resting on plants. *H. nilgiria* did not show special preference to any plant although was found resting on several plants. *H. serrata* and *H. consanguinea* have definite liking for neem (*Azadiracta indica*) and zizyphus (*Zizyphus jujuba* L.) among nearly 30 host plants on which they can feed.

Flight Range

L. coneophora did not move more than a meter from the place of emergence. It walked faster than many other chafer beetles. *H. nilgiria* was capable of flying long distance and was attracted strongly to light. *H. serrata* and *H. consanguinea* were also attracted to light, but they are not capable of flying long distance. Marked and released *H. serrata* beetles were recovered from light source at 660 m from the place of emergence, whereas they did not go beyond 150 m to preferred host trees in one night flight. More than 90% of the beetles were confined to within 50 m radius, if the preferred hosts were available at the place of emergence.

Egg Laying

All the species laid their eggs at a depth of five to eight cm irrespective of soil type and climatic conditions. Eggs were individually laid in earthen cells. Normally eggs hatched in 10 to 18 days but eggs may not hatch and remain viable under dry conditions, up to a month in the case of *H. serrata*, after which the eggs hatched in presence of moisture. If there was moisture four days after laying, the eggs hatched in 10 to 12 da, but the young ones did not come out of the earthen cell even up to 120 da until the surroundings got enough moisture, when the larva continued to lead normal life.

LARVA

Food Habits

The first stage larva of all the species fed on organic matter, unless they encountered roots. Only from the second instar, the grubs went in search of roots and their distribution confined to the root zones. *L. coneophora* were found mostly under coconut and arecanut (*Araca catechu*) plantations as they needed a larger quantity of roots. Although they are polyphagous, they were seldom encountered in grass, turf or under small plants, but had equal preference for tuber crops. The grownup larva reached up to 10 cm in length. *H. nilgiria* could feed on woody plant roots but were commonly encountered under coffee plants. *H. serrata* and *H. consanguinea* fed on a variety of plant roots except under puddled conditions. More grubs of *H. serrata* were attracted to onion, french bean and groundnut than sorghum, maize, guard and garlic.

Migration

There was no horizontal migration in the case of *L. coneophora* and *H. nilgiria* as they generally were found in dense roots and favorable soil conditions. *Holotrichia serrata* was found to move a maximum of 6 m under row crops and up to a meter in lawns from hatching to pupation. In sandy loam soils the larvae moved a longer distance compared to red soils and black soils with more percent of clay.

Vertical migration was maximum in the case of *L. coneophora* and *H. nilgiria* in laterite soils. Although eggs were laid at a depth of 5 to 8 cm the grubs were found to go up to 2 m before pupation, depending on the level of moisture in laterite soils during summer. The other 2 species pupated at depths varying from 20 cm in the Deccan Plateau in the case of *H. serrata* to 1 m in *H. consanguinea*. Similarly, in upper Simla Hills at altitude above 3000 m *Holotrichia* species went up to 1 m depth.

Effects of Moisture on Larva

Complete saturation of soil for more than 6 da was detrimental to grubs of *H. serrata*. In laterite soils grubs were not affected by continuous rain for several days, as there was enough aeration. A continuous wet season for nearly 2 mo during the monsoon in west coast and western ghats, did not affect the normal activity of *L. coneophora* and *H. nilgiria*. However *H. serrata* did not thrive well under this condition but had more chances of overcoming prolonged drought condition in the plains. The young larvae of this species did not come out of the earthen cell for up to 4 mo under drought condition and revived activity immediately when moisture was available. *H. consanguinea*, found in the range of 20 to 40 cm under normal conditions, but went deeper in sandy loam soils up to 1 m depth during summer as was found in Punjab. Under inundation resulting from continuous rain for a couple of days, the larvae came to the surface of soil and exposed the abdomen, dipping head and abdominal tip into the soil until the water receded when they went back to the soil.

PUPA

The pupal period of all the species of melolonthids listed have ranged from 2 to 3 wk. Pupation generally started in December -January in majority of the species but *L. coneophora* pupates in March-April and early May. In this case the adult life inside the soil was short compared to *Holotrichia* spp. which spends its life as an adult inside soil in the pupal cell for up to 6 mo, in some cases.

The depth at which pupation occurred depended on the type of soil and species involved. *L. coneophora* pupated at depth ranging from 1-2 m in laterite soil. *H. nilgiria* pupated at depths ranging from 30 to 100 cm. *H. consanguinea* usually pupated at depths around 30 cm but it was not unusual to find pupae at depths up to 1 m in sandy-loam soils.

Natural Enemies

Very few parasites and predators were recorded on either adults or grubs. Toads (*Bufo melanostictus*) feeding on adults and crows (*Corvus splendehs*) on grubs were the main predators.

The insect parasites include *Tiphiids* and *Scoliids* but at no time were they found to be abundant enough to check the white grubs.

The fungal pathogens *Metarrhizium anisopliae* and *Beauveria brongniartii* were found attacking all the stages of the pest. *M. anisopliae* was mostly found in the coastal belt during the monsoon when high humidity and high temperature prevailed. *B. brongniartii* was found to attack all the stages of the insect including grub, pupa, and adult in the transitional belt of high rainfall and low rainfall area. Up to 5% of the grubs were found to be infested with bacterial diseases under all situations.

DISCUSSION

There are nearly 200 species of white grubs in the sub-families Melolonthinae, Rutelinae, Dynastinae and Cetoninae of the family Scarabaeidae which are economically injurious to crops in India either in their adult stage or in larval stage or both. The genus *Holotrichia (Lachnosterna)* alone has more than 120 species known to occur in India (Frey, 1971), causing injury to plants mostly in their larval stage. Not all known species have become pests although their feeding behaviour is similar to that of the highly injurious species. The most widely distributed and destructive species are *H. serrata* and *H. consanguinea*. Both these are quite similar in their biology and behaviour. H. serrata is found throughout India whereas H. consanguinea is restricted to the northern part of India. These two species have assumed the status of national pests of crops in the last two decades in India. Some of the factors responsible for the outbreak of this pest in relation to agriculture is discussed here.

Up to 20 years ago, traditional agriculture closely followed the monsoon pattern in this country. Adults of white grubs (May-beetles or June bugs) also became active after the premonsoon rains. The annual life cycle of the pest started with egg laying after the premonsoon rains when preparatory cultivation also started. During tillage operations like ploughing, harrowing and sowing, grubs were reduced to a minimum due to predation by birds or injury. But with the shift in the cultivation practices brought about by the introduction of high yielding varieties of artificial irrigation in the early sixties, the availability of food changed for white grubs and the time of tillage.

White grubs are found in all situations where plant growth is possible except under puddled condition. There was a balance in nature in their population level when they were subsisting in uncultivated area. With extension of cultivated area, in the last 25 years, which has almost doubled the cultivated land to 167 million hectares, most of their habitat has been encroached upon. During the same period irrigation was extended from 18% to 25% of cultivated land. Consequently, growing crops do not depend on the monsoon and the sowing is done much earlier than the onset of rains. The problem of white grub was more severe in areas where there was a standing crop at the time of adult emergence. For example, sugarcane is traditionally planted during December-January. At the time of egg laying in May-June the crop is half grown with no possibility of disturbing the soil to expose the young ones for predation. Moreover, the injury is noticed only after 2 to 3 mo when the grubs are fully grown and conditions are favourable even for chemical control. Similar situations are encountered in the case of other crops like maize, sorghum, groundnut and vegetables (Veeresh, 1977) which are grown as relay crops whenever artificial irrigation is available.

Report of severe outbreak of white grub (H. seratta) was reported from Mahadeswarapura, Mandya District, Karnataka during 1974-76 in an area of 200 hectares. The pest was not encountered in the magnitude before in the living memory of the farmers of that area. Analysis of the situation revealed that the area was mainly cultivated with the help of rains before 1970. In the early 1970s, several irrigation wells were dug and growing crops almost round the year was started. Sugarcane became the major crop followed by sorghum and maize. The pest which was at low population levels confined to low lying areas, suddenly found a new situation where it could multiply and establish unharmed. In 2 to 3 yrs, it increased to a population level of 40 to 60 grubs per square meter. In the year 1976, a total of 1.4 million beetles were collected in this 200 hectare area. This was one of the few instances studied where shift in agriculture was the cause for the pest outbreak.

There was no report of any damage due to white grups from upper Simla Hills of Himachal Pradesh at altitudes ranging 2500 to 3000 m prior to the introduction of potatoes from the Central Potato Research Institute, Simla which evolved varieties to grow at high altitudes. The area under potato was extended to hitherto uncultivated areas. White grubs which were lurking in small numbers suddenly found the proper soil conditions with plenty of food during their larval period. Now the cultivators have to be content with only 60 to 80% of good tubers, the others scooped out by the grubs are either discarded or sold at very low prices.

The widespread distribution of white grubs is most man-made. The studies on the behaviour and biology revealed that the adults have a limited flight range; less than 660 m from the place of emergence. The larval migration is almost nil in many cases but then can go up to a maximum distance of 6 m depending on the types of crops or types of soil. Although the adults of Holotrichia have some hosts on which they feed by preference if available within a short distance from their place of emergence, they do not go in search of hosts over a very long distance. The widely distributed species H. serrata and H. consanguinea are attracted to light at the time of emergence. Perhaps increased transport systems in the recent past might have helped to some extent to carry the beetles at dusk from the place of their emergence to uninfested areas. It is common to see the incidence of white grubs greater on road side fields and in farms with electric lights.

Increased use of inputs like fertilizer and pesticides also has helped to increase the incidence of white grubs. According to Box (1935) the white grubs disappeared as such after the giant toad (Bufo marinus) was introduced to Puerto Rico but reappeared after the decline of toads due to a depleted food supply as a result of widespread use of pesticides. Modern agriculture in India, too, depends more on inputs like irrigation, fertilizer and pesticides to grow high yielding varieties. Their effect on the natural enemies of white grubs is not yet known but the pest is on the increase. This might be due to depleted natural enemies. In recent years, white grub in endemic areas in Maharashtra and Rajasthan have been covered with insecticide sprays on host trees of adult beetles for the control of white grubs (Raodev et al., 1976; Yadava et al., 1978). At several places, birds were noticed dead after eating these beetles. In a survey made in Nandad district of Maharashtra to find out the causes of severe outbreak of white grub in that area, several farmers were complaining that they have not been seeing the crows following their plough at the time of ploughing as they used to be some years back. No one was able to give the reason for the same.

Some species are restricted to a particular region, as for example; L. coneophora and H. nilgiria are found in the heavy rainfall track of low laying region and at high altitudes, respectively. Both thrive well on laterite soils whereas H. serrata although present in these regions has not been able to establish as a major pest as it cannot manage to live in the lateritic soils.

CONCLUSIONS

From the results obtained during the course of these observations, it can be concluded that man-made situations have helped the pest to multiply and spread despite weak innate ability to migrate and disperse. Adult dispersal is mostly localized, unless it is aided by external agencies. The larval migration is negligible except where the roots are sparse; then they may move a few meters. Both adults and larvae have few natural enemies. Heavy mortality occurs only in situations where the infested soil is disturbed repeatedly and grubs are exposed to predators or injured. Lands kept under crops at the time of egg laying that provide roots with adequate and continuous moisture with least distrubance of soil during larval period will favour the buildup of the pest. Bringing uncultivated area under crop, extending irrigation to unirrigated areas, relay cropping, and pesticides have contributed favourable conditions for the pest outbreak.

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THE INFLUENCE OF AGRICULTURAL LAND USE PRACTICES ON THE POPULATION DENSITIES OF *Allolobophora trapezoides* and *Eisenia rosea* (OLIGOCHAETA) IN SOUTHERN AFRICA

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INTRODUCTION

As soon as soils are utilized for agricultural purposes it is generally accepted by many soil biologists that a decrease in the number of soil organisms as well as species diversity will follow (Evans & Guild, 1948; Graff, 1953). According to Ghilarov (1973) very few members of the soil community can survive the destruction of soil structure resulting from cultivation. Earthworms are affected in various ways by cultivating practices depending on the species and frequency of cultivation (Edwards & Lofty, 1973). The latter authors recorded increases in the numbers of certain species. They presumed that a modest amount of cultivation provides better soil conditions for earthworm burrowing. Allolobophora caliginosa was favoured most in the long run by cultivation practices. In later studies the same authors (Edwards & Lofty, 1977) found that earthworm populations have been consistently larger in uncultivated plots than in cultivated ones with L. terrestris populations particularly favoured by lack of cultivation. For this species, in particular, decreases of up to 400% were recorded while cultivation decreased populations of other species of earthworms much less.

The influence of chemical fertilizers on the soil fauna has not yet been studied extensively since the work of Duerell (1959) and Slater (1954). Artemjeva & Gatilova (1973) completed a long term investigation in Russia and concluded that chemical fertilizers such as ammonium sulphate, superphosphate and potassium chloride have a direct negative effect on the soil microorganisms, depending on dose of application (and of course, relative composition). These authors are convinced that the nature of the effect of a mineral fertilizer is also determined by the type of plant cover. Zajonc (1973) also concludes that high doses of lovosice niter affects earthworm numbers adversely.

The present investigation was undertaken in irrigation soil in South Africa as part of a wider survey to evaluate the position of the endemic and introduced earthworms in agricultural soil in the Mooi River irrigation area (Visser & Reinecke, 1977). The irrigation area houses various earthworm species of which Allolobophora trapezoides has the highest population density followed by Eisenia rosea with the widest distribution in the area. The purpose of this study was to demonstrate the collective influence of some agricultural land-use practices on the earthworm fauna.

METHODS

Research was conducted on two adjacent sampling sites (A and B) of 50m x 100m in the Mooi River irrigation field near Potchefstroom (27°4'E and 26°47'S). Medicago sativa (luzern) had been established three years previously. The particular spot proved to have the highest population densities for A. trapezoides and E. rosea in the irrigation area (Visser & Reinecke, 1977). The maximum crop yield for the field was 1,91 kg/m^2 in 1975. The two adjacent sampling sites were carefully selected and analysed faunistically, physically and chemically to ensure the closest possible similarity.

Thermographs were erected on the sampling sites to measure soil temperatures at a depth of 15 cm during the research period. Rainfall was measured with a conventional funnel-type rain gauge. Random soil samples were taken from both sites for chemical analysis. Conductivity (Boujoucos-method) and pH (KCl-method) were also determined. Physical descriptions were obtained for soil samples from both sites. The hydrometer method was used to analyse particle size before classifying textural classes (Townsend, 1973). Complete profile descriptions were provided by pedologists from the P.U. for C.H.E. at Potchefstroom. Measurements of soil pF (Lavelle, 1971) for both sites were obtained with the aid of a membrane press (plate extractor). Soil moisture content was determined every second week with the aid of an Ultramat moisture meter using soil samples taken at a depth of 15 cm.

To determine the number of samples to be taken from each site, a preliminary survey was undertaken. Southwood's (1966) formula was employed to determine the number of samples required to calculate the mean density (at 95% confidence level) within 20% of the actual mean density. From this survey five samples proved adequate. However, eight were taken from each site over a period of 15 months from October 1974 to December 1975 after a preliminary evaluation in September 1974. The samples were taken at random using tables for random distribution. These eight soil samples of 25 cm^2 were taken every second week from each of the sampling sites. This sample size proved practical (Zicsi, 1958; Atlavinyte, 1964; Tsura, 1975; Reinecke & Ljungstrom, 1969) and statistically reliable.

Earthworms were extracted from the soil samples by handsorting on a field table. Samples were taken to a depth of 40 cm and sometimes deeper, depending on soil moisture conditions. The collected worms were kept alive on moist filter paper. Biomass determinations were undertaken on live worms after no more castings were excreted. Satchell (1969), Madge (1969), Block & Banage (1968) and Nordstrom & Rundgren (1972) have shown that preserved specimens could lose as much as 25% of their body mass.

Site B was disturbed physically as a result of cultivation practices. Crop rotation took place and a NPK-fertilizer was applied. This happened in October 1974 and again in August of the following year. Site A was left undisturbed through the whole of the research period. The application of these land-use practices to site B took place shortly after it became clear that the two sites were, for all practical purposes, qualitatively and quantitatively identical.

The results of the survey were subjected to a variance analysis programme BMDP2V by die Computer Centre, P.U. for C.H.E. using an IBM 370'125 computer.

The tolerance of _A. trapezoides_ for the various components of a NPK-fertilizer was investigated by subjecting batches of mature worms to various concentrations of commercial potassium chloride, superphosphate and ureum separately. The aim was to gain a provisional insight into their susceptibility for the various components in order to draw some conclusions on the possible role of fertilizers as a disturbing factor operating in site B. Eight batches of 15 worms each were kept in glass jars at concentrations of 200 ppm through to 4000 ppm KCl for 10 hrs in a controlled environment. Worms were thereafter washed and placed on wet filter paper in petri dishes. They were investigated for mortality after 24 hrs. The same procedure was repeated with ureum and superphosphate. Provisional conclusions are mentioned in the discussion of this paper. An in depth bio-assay is presently being undertaken by J.R. Kriel and the senior author at this institute.

RESULTS

Comparison of Two Sampling Sites

Strictly identical soil profiles were obtained for both sampling sites. The A horizon (ortic) (0-34 cm) had a sand loam texture, apedal structure with high porosity. B_{21} was neokutanic (35-66 cm), sand loam but structurally less developed. Earthworm burrows were predominantly in A_1, sometimes in B_{21} and very rarely in B_2. A complete analysis is given by Visser (1978). The physical properties of the soils from the two sampling sites are compared in table I.

The chemical properties of the soils from the two sampling sites are compared directly before and after site B was cultivated and a 2:3:4 fertilizer applied (5,3%N; 8%P; 10,7%K) at 200kg/ha (Figure 1). From the figure the similarity in the chemical make-up for the more important ions before cultivation can be clearly seen. After cultivation and fertilizer application soils from site B differed prominently in respect of K-content. Phosphorus almost doubled from 34 before to 70 p.p.m. after fertilizer application. The organic matter content remained the same and no fine analysis of nitrogen content was undertaken.

A comparison of the moisture conditions prevailing in the two sampling sites during the course of the investigation is illustrated by Figure 2. From this figure it can be seen that the available soil moisture conditions differed only slightly between sites A and B. The pF values are also indicated.

Quantitative Changes in Sites A and B

From the start of the survey in September 1974 the earthworm fauna of the two sites were quantitatively fairly similar. This remained so until October 1974. Site B was first cultivated the second week of October. The mechanical dis-

TABLE I. Comparison of the physical properties and soil moisture of the soils of sampling sites A and B at various depths.

Site	Depth (cm)	Conductivity (µS)	pH	% Silt	& Clay	% Sand	Text Class	% org. mat.	mean ± SE % moist.at kPa 33	1000	1500
A	0-35	0,82	7,3	15	11	74	Slm	7,12	6,6±1,3	5,6±1,4	4,4±1,3
	35-65		7,2	15	14	71	Slm	7,01			
	65-90		7,1	14	20	66	Slm	6,62			
	90-110		7,0	15	18	67	Slm	4,10			
B	0-35	0,79	7,2	16	8	76	Slm	6,37	7,2±0,2	5,6±1,5	4,7±0,6
	35-65		7,1	17	11	72	Slm	7,21			
	65-90		6,9	13	19	68	Slm	5,43			
	90-110		7,0	18	15	67	Slm	3,21			

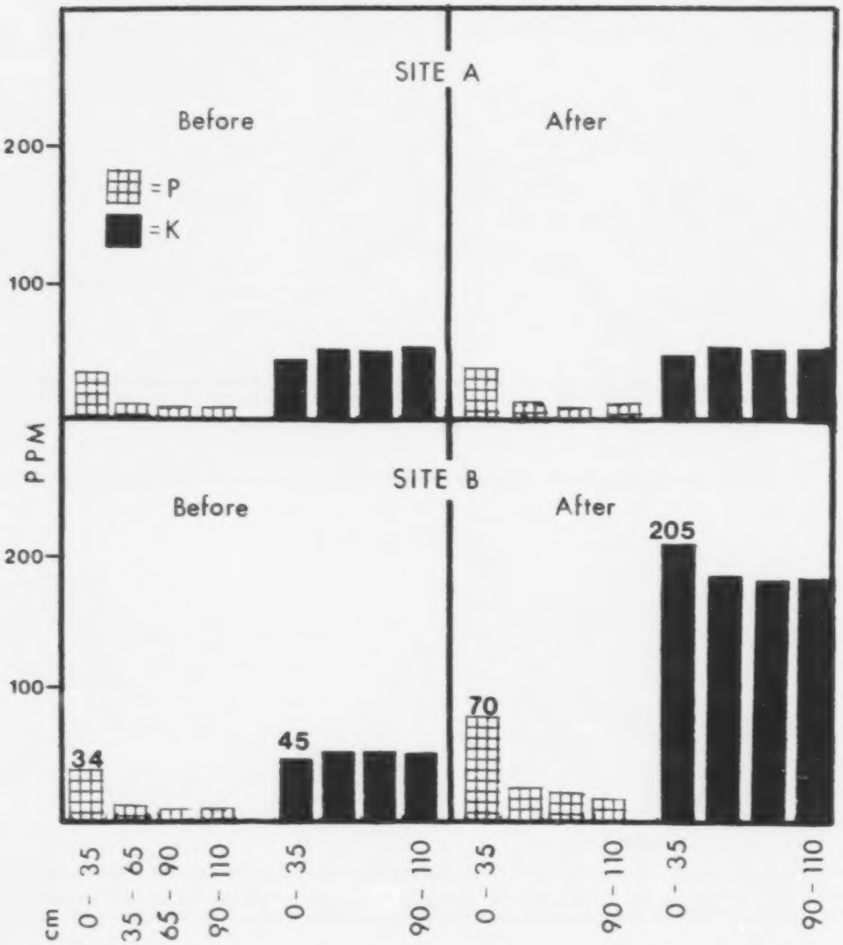


FIGURE 1. The concentration P and K in the soils from sites A and B before and after cultivation and fertilizer application (2:3:4 at 200 kg/ha) had taken place in site B. No significant change occurred in respect of Ca, Mg and Na content during the period.

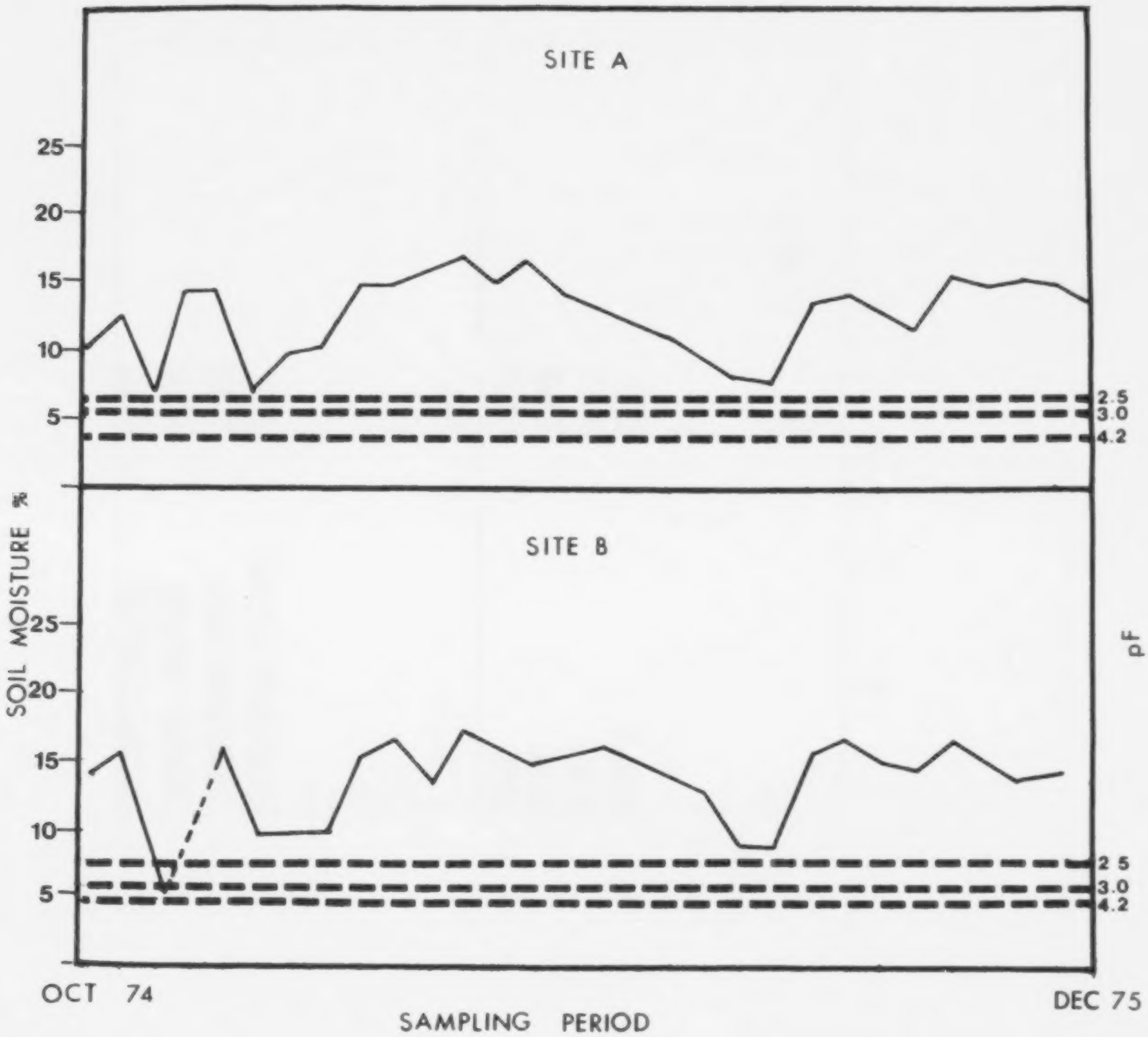


FIGURE 2: A graphic representation of the moisture conditions in sites A and B during the sampling period.

turbance to a depth of approximately 25 cm was accompanied by the application of a N.P.K.-fertilizer (2:3:4) at 200 kg/ha. Soil analysis in the area undertaken afterwards by a local fertilizer company lead them to recommend 1:4:0 combination at 200 kg/ha.

An immediate effect was observed, most probably caused by the combined effects of mechanical and chemical disturbances (including crop rotation). This was revealed by population estimates for both species (Figure 3). There was a dramatic decrease in the population density in site B. These populations only regained their original peaks in March and May with a maximum peak of 182 worms/m^2 in May for both species. The worms in the undisturbed site (A) reached a population density exceeding 600 worms/m^2 in mid-April. Both sites experienced a drop in numbers in June and July. These, however, correlated well with low rainfall data (Figure 3) and relatively low moisture conditions which prevailed on both sites. The same quantitative overall difference is revealed by the biomass figures for both species in both sites (Figure 4). The fluctuation patterns were basically similar for both sites.

Variance analysis (Visser, 1978), not represented here, confirmed a highly significant difference (at the 1% level) for the population densities of the earthworms in the two sampling sites. Comparison of the numbers of juvenile worms from the different sites were not very revealing and no major differences in reproduction rates were detected. It was, however, possible that the reproduction rate (as deducted from cocoons production and the number of juveniles sampled) of *A. trapezoides* was slowed down to a lesser extent in site B than that of *E. rosea*. From this and the fact that *A. trapezoides* was numerically affected to a lesser degree by the chemical and physical disturbances of the habitat it is concluded that this species seems to be more tolerant of changes in the habitat. This seemingly higher adaptability to disturbances may also correlate with the ability of this larger of the two species to migrate deeper down into the soil where it is less adversely affected by superficial changes in the upper soil layers.

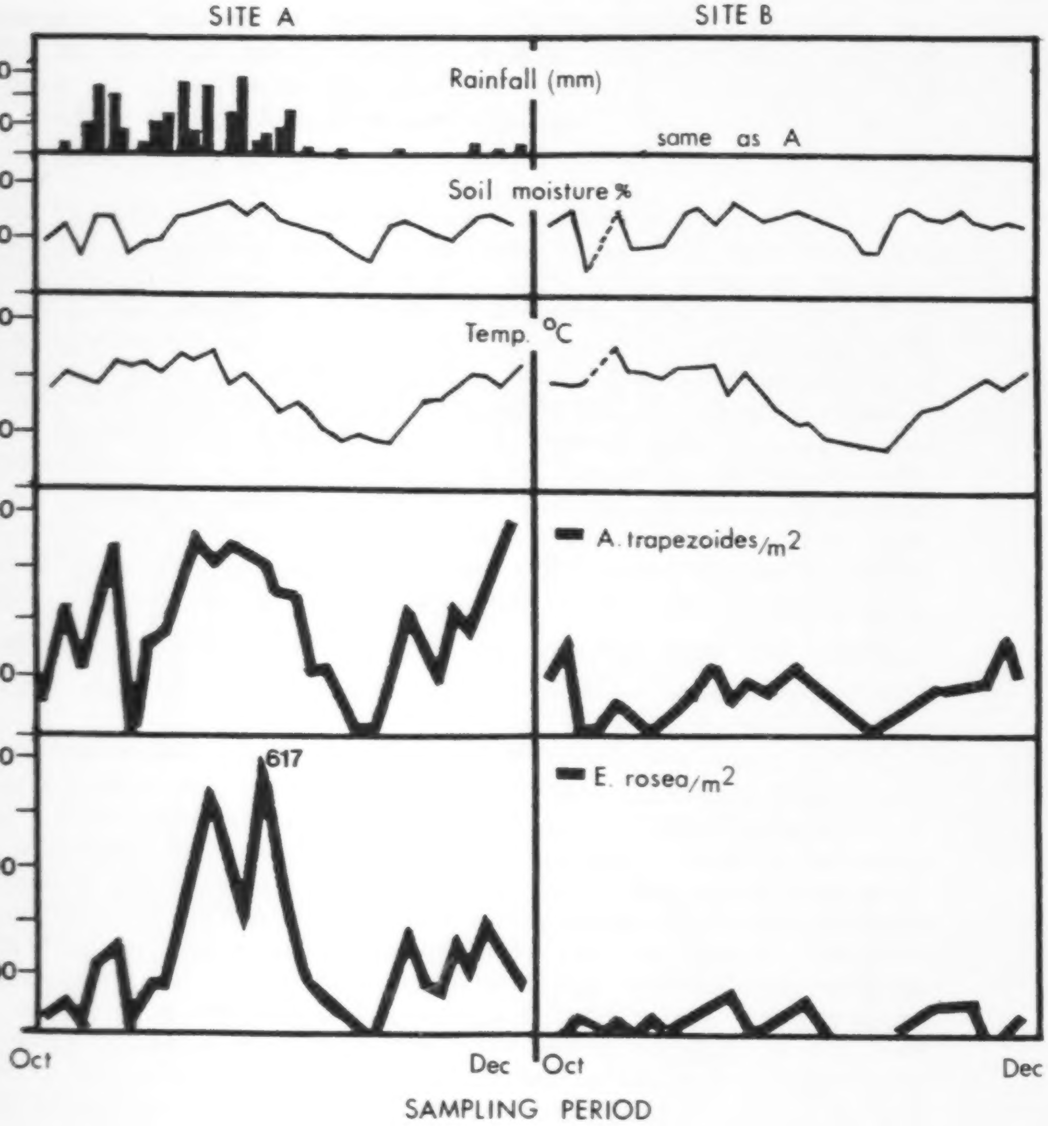
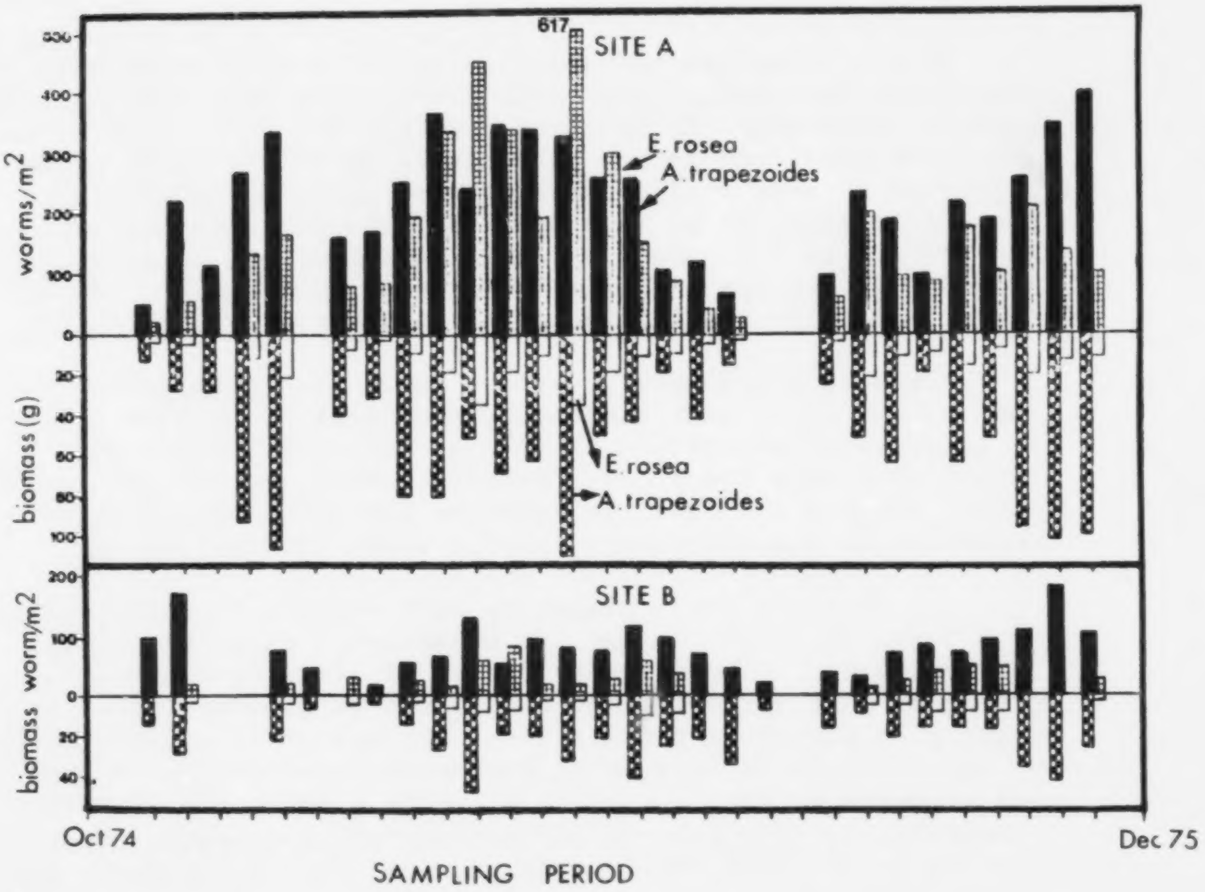


FIGURE 3. Graphic representations of the changes that occurred in the population densities of Allolobophora trapezoides and Eisenia rosea in sites A and B. Seasonal changes in rainfall, soil moisture content and temperatures are also given. All measurements and samples were taken at two-weekly intervals.

FIGURE 4. Histograms showing the seasonal changes in population density and biomass for A. trapezoides and E. rosea in sites A and B.



DISCUSSION

The overall effect of the land-use practices on the earthworm population densities of the two species for the period under consideration, is clearly revealed by the present investigation. Although this phenomenon is not new, it at least provides a scientific basis as far as effects on these earthworms are concerned.

Trials to assess the relative roles of crop rotation, fertilizer application and cultivation separately are at present under way. Indications are that KCl fertilizer in its commercial formulation only causes mortality in _A_. _trapezoides_ at extremely high doses. These doses are much higher than those measured in Site B of the present investigation. It seems to be the same with superphosphate, the application of which is accompanied by a lowering of pH to levels beyond the normal tolerance limits of the earthworms.

A possible synergestic effect could also operate between the various fertilizer components when applied in combination. This merits investigation as well as the invluence of soil type on possible toxological effects. Long term trials can only reveal whether the possible negative influence of fertilizers mentioned in the literature is of a short duration only.

The relative roles played by each component of the collective land-use practices can not be assessed from the present field studies. However, destruction of soil structure as a result of cultivation cannot be ignored as a major factor in destroying earthworm populations. Minimal or zero cultivation of agricultural land is being increasingly adopted as standard practice in many countries (Edwards & Lofty, 1977) with exceptionally good results and without any noticeable negative effects on the soil fauna. The physical soil environment and the destruction of its structural make-up may still prove the major contributing factor in eliminating or decreasing earthworm populations in agricultural soils.

In southern Africa endemic species are almost without exception absent from agricultural fields while the "common field worms" are either _Allolobophora_ _trapezoides_ or _Eisenia rosea_, but usually both. Laboratory trials and efforts to rear endemic species are extremely sensitive to changes in the physical environment as well as various forms of physical disturbances. It is common knowledge amongst farmers in many parts of southern Africa that endemic earthworms originally occurring in the soil, will disappear completely soon after a new agricultural land is cultivated. Du Plessis (1978) is convinced that the sensitivity of the endemic fauna for habitat changes and the human land-use practices in South Africa are leading to a destruction of natural populations. This contention seems to support the idea of Ljungstrom (1972) that man is playing a major role in exterminating the endemic earthworm fauna.

ACKNOWLEDGMENTS

The authors are indebted to the South African Department of Agricultural Technical Services for financial assistance and to prof. P.A.J. Ryke for his useful comments and the facilities placed at our disposal.

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QUESTIONS and COMMENTS

G. KLEE: Did you notice any bird predation of earthworms of freshly plowed soil in your study plots?

A.J. REINECKE: Due to the depth of ploughing very few earthworms were found on the surface directly after ploughing and no bird predation was noticed. If limited bird predation did occur, the effect could hardly account for the drastic changes in the population densities.

J.E. SATCHELL: Could the reduction in earthworm populations after cultivation have been caused by reduction of their food supply?

A.J. REINECKE: This could be a possibility although the fairly homogenous distribution of organic material in this soil and the earthworm's ability to move about should rule out lack of food as a direct cause. Structural changes in the soil as a result of cultivation may however still retard normal mobility and feeding.

S.E-D.A. FAIZY: I want to know your opinion regarding the following statement "High dressing of N-fertilizers only will reduce the density of soil fauna. However with a high dressing of a balanced NPK-fertilizer, the density of soil fauna might not be reduced."

A.J. REINECKE: The application of N-fertilizers are usually accompanied by a decrease in pH which is harmful to earthworms. A high dressing of balanced fertilizer will probably not reduce the fauna when the N-component is relatively low. I do not know of any available data to support the idea that the presence of (say) P and K would have a synergistic effect.

THE INFLUENCE OF FARMYARD MANURE AND SLURRY ON THE EARTHWORM POPULATION (LUMBRICIDAE) IN ARABLE SOIL

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ABSTRACT

Earthworms were sampled spring and autumn in the years 1976 to 1978 by formalin extraction and handsorting. Farmyard manure and slurry were given in the following quantities; 50 and 100 tons/ha each year, 200 tons/ha each second year and 400 tons/ha each fourth year. In this way both short term and long term effects were studied. Earthworms were identified, sorted into classes and measured as to biomass (fixed material).

The two types of manures greatly influenced the frequencies of individual species. Farmyard manure favours all species, especially *Allolobophora longa Ude, 1886*, whereas by slurry treatment *A. longa* is outnumbered by *Allolobophora caliginosa Savigny, 1826*. The greatest population densities are recorded by 100 tons/ha/year to 200 tons/ha /second year, for both types of manures. Following application of 400 tons manure/ha a sharp decrease in population size is seen. Two years after application of this amount of manure, the population seems to have recovered. Population size, however, is influenced by climatic conditions.

INTRODUCTION

Over the past years a great number of studies has been carried out on the importance of earthworms in arable soil and the influence on earthworms of mechanical treatment, straw incorporation, green manuring and animal manure, some of which are cited here: (Barley and Jennings, 1958; Dunger, 1969; Edwards, 1975; Edwards and Lofty, 1976; Graff and Kuhn, 1977; Leger and Milette, 1977; Rogaar and Boswinkel, 1978; Schwerdtle, 1969; Sharpley and Seyers, 1977; Seyers, Sharpley and Keeney, 1979; and Wilcke, 1962).

Studies on animal manure have mostly been concerned with the traditional semisolid farmyard manure (FYM). However, with the introduction of modern technology into husbandry it has become more convenient to collect faeces and urine from the livestock in tanks, stored as a liquid suspension - slurry, which is spread on the fields as a manure or as simple waste. This practice may, however, result in the spreading of pathogens, and slurry has also been shown to be toxic to earthworms under certain conditions (Currey, 1976).

In the present study is reported on the influence of high dosages of slurry and FYM on earthworms under field conditions. The investigations were carried out in the period 1976 to 1978 on Askov Research Station, Southern Jutland, Denmark, and were supported by the Danish Research Council, SJVF.

METHODS and MATERIALS

The soil type of the experimental fields of Askov Research Station is a sandy loam with a weakly developed eluvial horizon below the ploughing layer (Andersen in press). Samples were taken in the L - field, which is under conventional tillage with winter ploughing, normal preparation of seedbed in spring and a yearly rotation of cereals, sugar beets and grass.

The experiments with farmyard manure and slurry were started in 1972. Farmyard manure and slurry are given to the plots in the following amounts: 50 and 100 tons/ha each year, 200 tons/ha each second year and 400 tons/ha each fourth year. These amounts are equivalent to 250, 500, 1000 and 2000 kg N/ha, calculated from Nemming, 1976. A control was included, receiving NPK fertilizer, 80 kg N/ha. In December 1976 all the above mentioned levels of manures were given.

Earthworms were sampled by the formalin method from a 0.5 m^2 sampling quadrat. 2 x 10 litres 0.4% formalin solution was used per quadrat. Formalin extraction was supplemented by top soil handsorting. Sampling was performed in spring, April to May, and in autumn, October, at presumed maximum activity of earthworms. There were four plots per treatment of approximately 70 m^2 size. Two sampling units were taken per plot, yielding a total of eight sampling units per treatment. The standard error of the mean by this number is between 10 and 20%. Sampling was made in October 1976, April 1977, October 1977 and October 1978. (I) and (II) in Table 1 and 2 refer to April and October respectively.

Biomass of earthworms was determined on specimens fixed in 4% formalin stored in 70% alcohol. No allowance was made for gut content and weight loss in the storage liquid. The earthworms were sorted into: 1) mature worms with clitellum present and 2) worms without clitellum present.

Five species of earthworms were commonly found and identified (Stöp-Bowitz, 1969) as *A. longa*, *A. caliginosa*, *A. rosea Savigny, 1826*, *A. chlorotica Savigny, 1826* and *Lumbricus terrestris L. 1758*.

As to *A. caliginosa* material from Fyn collected simultaneously with that of Askov makes it probable (Gates, 1972) that the Askov material of *A. caliginosa* should be referred to as *Allolobophora turgida Eisen, 1874*, and the Fyn material to *A. tuberculata Eisen, 1874*, the latter being consistently larger than *A. turgida*. Probably also *A. trapezoides Duges, 1828*, may be found in the Askov material.

RESULTS and DISCUSSION

Table 1 and 2 show the total number and biomass of earthworms/m^2 per year, including the NPK fertilizer control, while in Table 3 the combined effect of all years is given for the respective levels of manures and in Table 4 correspondingly for the different species.

TABLE 1. Total biomass, g/m^2 of earthworms, at different levels of farmyard manure and slurry, collected in October 1976, April 1977, October 1977 and October 1978. Askov Research Station.

	FARMYARD MANURE				SLURRY			
	76_{II}	77_{I}	77_{II}	78_{II}	76_{II}	77_{I}	77_{II}	78_{II}
CONTROL	13.2	22.6	22.0	17.3	13.2	22.6	22.0	17.3
50 t	11.6	14.5	25.2	41.5	11.4	19.6	23.8	40.1
100 t	23.5	23.2	37.3	39.7	13.1	26.4	34.1	35.4
200 t	15.2	27.7	41.1	38.1	10.8	19.7	22.1	34.0
400 t	12.0	21.6	32.8	39.6	9.0	19.1	19.1	39.2

TABLE 2. Total number of earthworms/m^2. Other data as in Table 1.

	FARMYARD MANURE				SLURRY			
	76_{II}	77_{I}	77_{II}	78_{II}	76_{II}	77_{I}	77_{II}	78_{II}
CONTROL	101.1	122.9	150.8	131.3	101.1	122.9	150.8	131.3
50 t	143.0	119.0	242.7	228.9	126.9	118.0	291.6	255.8
100 t	216.4	148.7	294.1	214.4	153.4	135.4	385.4	272.8
200 t	178.0	209.4	284.8	228.8	150.0	140.5	352.0	282.4
400 t	128.3	117.6	176.9	452.9	132.9	78.6	144.8	383.3

The combined effect of the two types of manures was tested by Students t-test to each other and to the control receiving 80 kg N/ha.

Along the same lines Figures 1 to 3 show the individual effect of manuring on the five collected species.

A. longa is favoured by FYM with a number per m^2, which is significantly above the number found in control plots, while slurry reduces the number of *A. longa* to a remarkable degree (Table 2). The high number of *A. longa* found in FYM compared to control plots is caused by an increased reproductivity (Andersen in prep.). Thus there appears to be a fast turnover of juvenile *A. longa* in FYM probably influenced by the mechanical treatment, preventing a greater proportion of the juveniles to reach maturity.

L. terrestris, the second, large species, is only found in low numbers. This species also benefits from the FYM, and biomass here as well as numbers are significantly above controls. Because of its very large size it yields 19% of the total biomass in FYM. As in *A. longa* number is reduced by slurry treatment.

Both *A. longa* and *L. terrestris* possess well defined openings of their burrows and on application of slurry this will infiltrate the burrows and either kill some of the worms in the burrows or force them to the surface, where they may perish, which has often been observed in the field. The other three species, which do not possess well defined openings of their burrows are not exposed to the direct influence of slurry to the same extend. Juveniles which in general are closer to the surface than adults will also suffer more from the direct action of the slurry.

A. caliginosa is the dominating species by number in both FYM and slurry, including control. This species is greatly favoured by slurry as well as FYM treatment, where numbers are significantly above controls (Table 4). The most marked inflecence is seen in slurry, where the biomass is significantly above both FYM and control. The biomass in FYM is not significantly different from that of control plots.

A. longa and *A. caliginosa* seem to vary inversely as to number, and the reasons for this are, 1) that *A. caliginosa* is less exposed to the direct influence of slurry as explained above, 2) that *A. longa* and *A. caliginosa* show different food preferences. Both species ingest considerable amounts of mineral soil, but besides *A. longa* seems to prefer the more particulate (more or less decomposed plant debris) organic matter of FYM, which is not found in similar condition in slurry. *A. longa* has also been shown actively to seek up particles and clods of sewage sludge incorporated into the soil (Andersen in press). *A. caliginosa* on the other hand is a consumer of humus, which may fit well with a soil where growth of bacteria and other microorganisms has been stimulated after the application of slurry (Figures 1 to 3).

A. rosea and *chlorotica* seem not to be greatly influenced by the two types of manures, and data for these two species have therefore been combined in Table 4. Biomass in both slurry and FYM plots

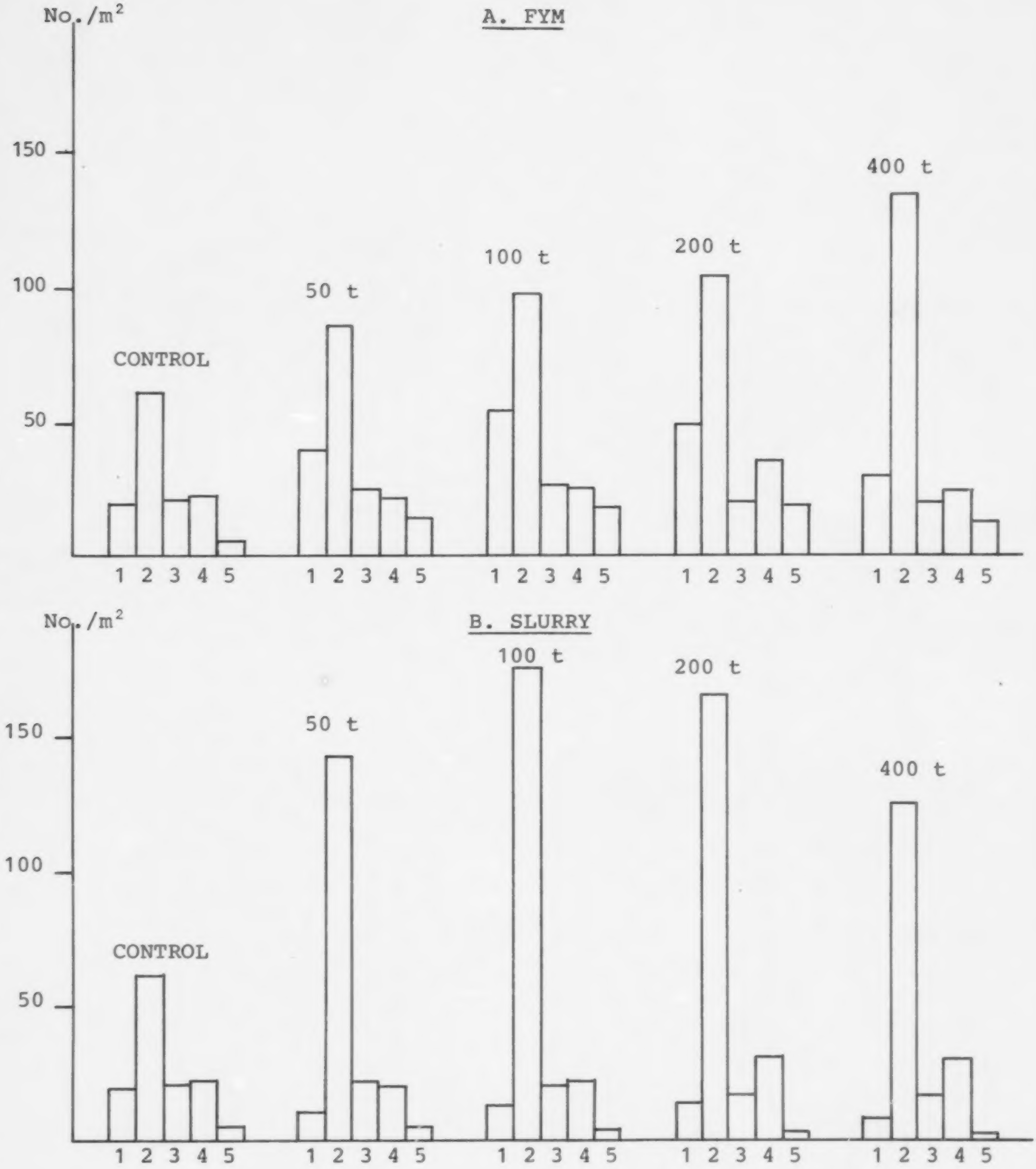


FIGURE 1. Influence on individual earthworm species of different levels of manure. A. Farmyard manure, B. Slurry. Number/m^2 of 1)*A. longa*, 2)*A. caliginosa*, 3)*A. rosea*, 4)*A. chlorotica*, 5)*L. terrestris*. Mean of data from October 1976 to October 1978.

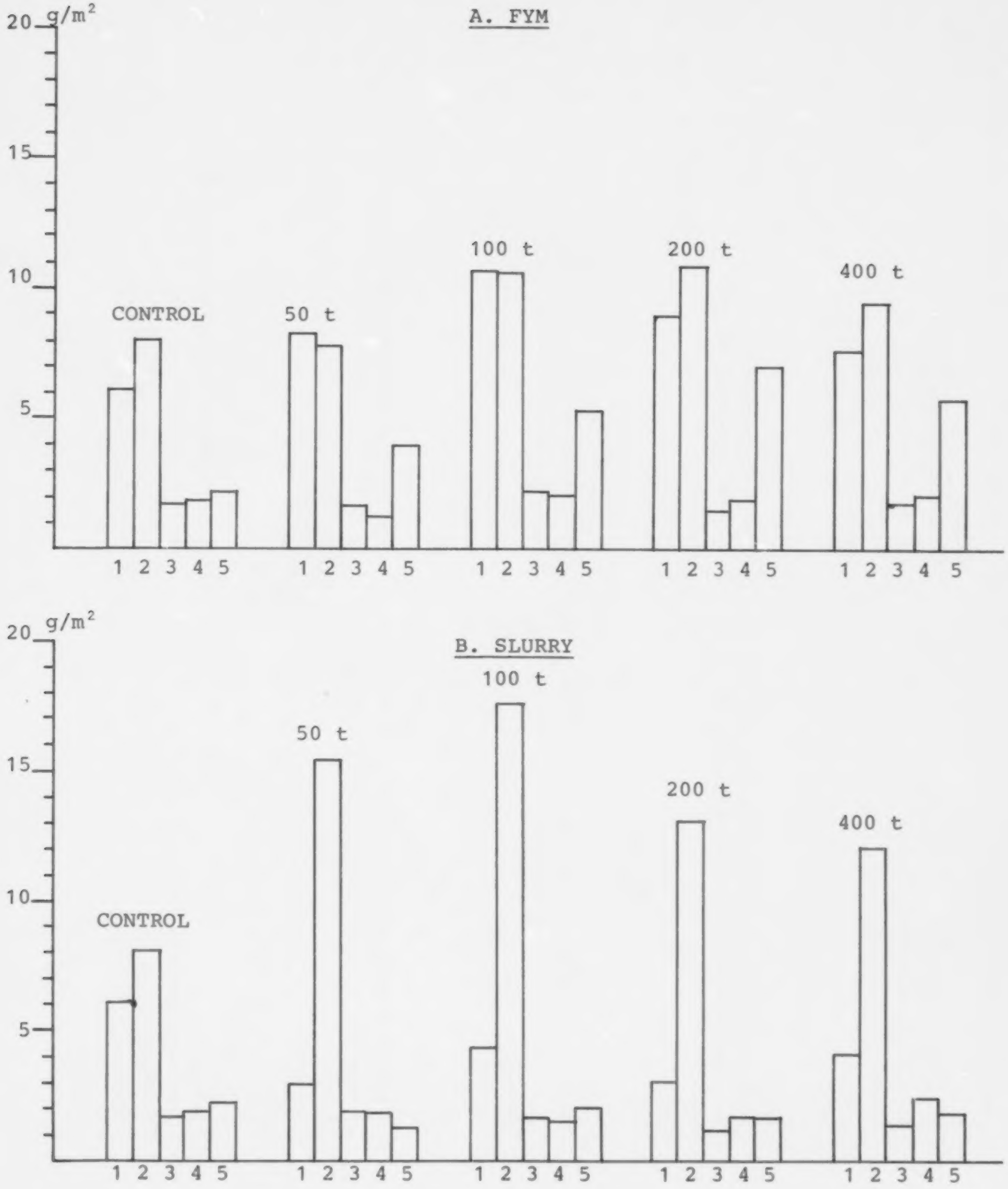
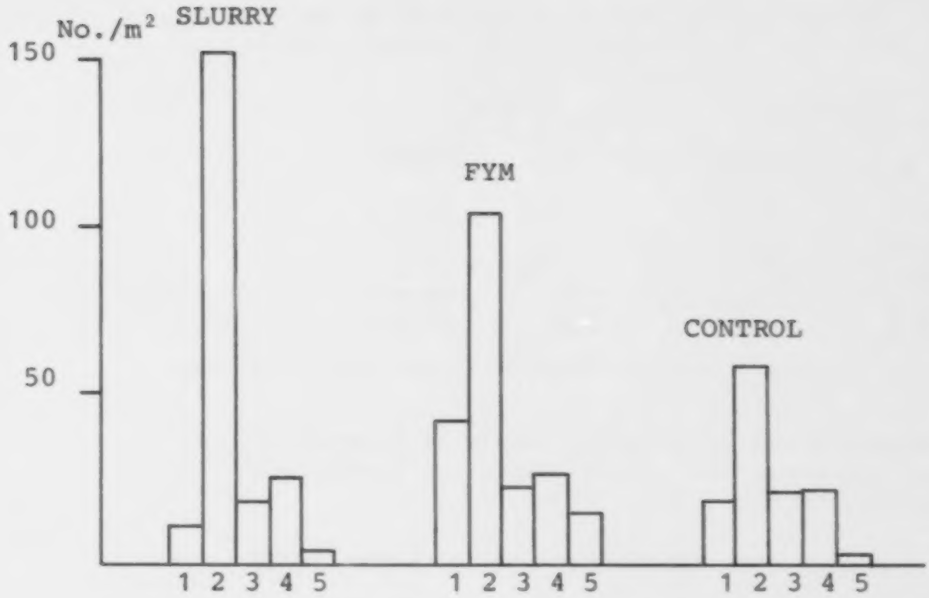


FIGURE 2. Biomass of earthworms, g/m². Other data as in Figure 1.

A. No.



B. BIOMASS

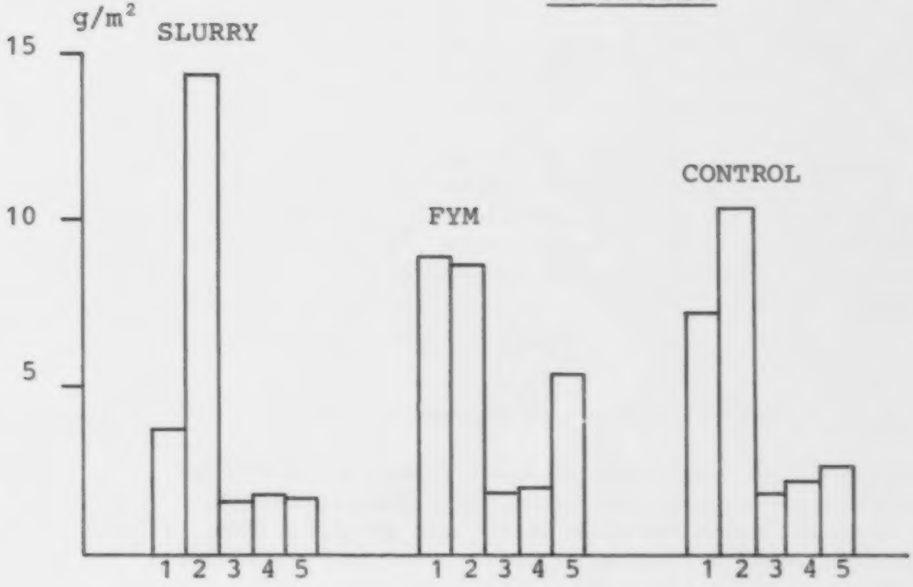


FIGURE 3. Influence of farmyard manure and slurry. A. No./m^2. B. Biomass g/m^2. From data shown in Table 4. Earthworm species as in Figure 1.

TABLE 3. Total number and biomass g/m^2 of earthworms at different levels of farmyard manure and slurry expressed as the mean of data from October 1976 to October 1978. Tables 1 and 2.

	No./m^2		g/m^2	
	FYM	SLURRY	FYM	SLURRY
CONTROL	126.5	126.5	20.0	20.0
50 t	183.3	199.1	23.2	23.2
100 t	218.4	236.7	30.9	27.2
200 t	225.2	231.2	40.0	20.7
400 t	218.9	184.8	26.5	21.5

TABLE 4. The combined effect of different levels of farmyard manure and slurry given as the mean of number and biomass g/m^2 from October 1976 to October 1978.

		TREATMEMT			SIGNIFICANCE		
		SLURRY	FYM	CONTR.	S/C	F/C	S/F
A. longa	g/m^2	3.80	8.90	7.24	+++	-	+++
A. caliginosa		14.44	8.70	10.41	+++	-	+++
A. rosea + *A. chlorotica*		3.38	3.88	4.04	+	-	++
Lumbricus terrestris		1.68	5.42	2.70	+	++	+++
Total		22.30	27.90	24.40	-	+	+++
A. longa	No./m^2	11.50	42.62	18.68	+++	+++	+++
A. caliginosa		153.08	105.00	59.96	+++	+++	+++
A. rosea + *A. chlorotica*		43.36	50.92	43.82	-	++	+++
Lumbricus terrestris		3.74	15.26	4.74	+	+++	+++
Total		206.68	213.82	127.22	+++	+++	-
Degrees of freedom					(154)	(154)	(254)

was lower than control, but the number was highest in FYM.

The total number of earthworms is equal (Table 4) in FYM and slurry, and significantly higher than in control. The highest biomass is seen in FYM, whereas biomass in slurry was slightly lower than in control. This small difference, however, was not significant.

In *A. caliginosa* the proportion of adults is 10% in both FYM and slurry, but 26% in control (Andersen in prep.). In *A. longa* the respective percentages are 10, 3 and 13. The number of adults is not very different between the two types of manures and control, and an increased reproduction appears to be the main effect of the manure. Slurry increases only the *A. caliginosa* population, whereas FYM in general favours all species.

The reason why total number of adults does not increase, corresponding to the increased reproductivity, probably lies in the fact that the mechanical treatment levels off population size each year.

Therefore the resulting biomass in the two types of manures is not very much different from controls, although biomass in FYM (Table 4) is significantly greater than biomass in slurry. The main reason for this is the contribution by 19% from *L. terrestris* in FYM as opposed to only 7% in slurry, and the negative effect of slurry on the two largest species *A. longa* and *L. terrestris*.

A more detailed picture of the influence of the two types of manures is seen when the influence of the different levels of manures on population size is studied. In FYM *A. longa* and *A. caliginosa* are dominating with respect to number, and it is seen that the number of *A. caliginosa* is increasing with increasing level of FYM (Figure 1). With respect to biomass *A. longa* and *A. caliginosa* are equally important, and the maximum values are reached (Figure 2) at 100 to 200 tons FYM/ha. Also the biomass of *L. terrestris* is great at these levels.

In slurry *A. caliginosa* is the sole dominating species. The maximum number and biomass are reached at 100 tons/ha (Figures 1 and 2). The maximum value for total number and biomass is seen at 100 to 200 tons slurry/ha (Table 3).

Short term effects are seen in the spring of 1977 after application in December 1976 of the different quantities of manure (Tables 1 and 2). For 50, 100 and 200 tons there are no significant differences in the number/m^2. But at 400 tons there is a decrease in the number of *A. caliginosa* with up to 50% in slurry. In October 1977 and in October 1978 very high values are recorded in both FYM and slurry. This is caused by an enormous hatching of new individuals.

The biomass seems contrary not to be affected in the same way (Table 2), which indicates that a short term effect is mostly seen in the juvenile individuals on application late in the year. These are generally encountered in the more superficial layers of the soil profile compared to adults, because of reduced burrowing capabilities. Therefore juveniles will be more exposed to the direct influence of the manures on the time of application in December, where the adults have moved deeper into the soil.

It is seen that a general increase in both number and biomass has taken place from 1976 to 1978 (Tables 1 and 2). The low levels of number and biomass seen in October 1976 were probably caused by severe summer drought in both 1975 and 1976. The influence of climatic conditions are best seen in control plots and in plots receiving manure each year i.e. 50 and 100 tons/ha. In the spring of 1977, compared to October 1976, there is a greater biomass (Table 1) in these three treatments, whereas total number (Table 2) is little changed or slightly lower. This is consistent with other studies (Rundgren, 1977), showing that in spring the number in general is lower than in autumn in temperate regions. In October there is a further increase in biomass at 50 and 100 tons/ha, whereas biomass in control is unchanged. This is caused by the greater amount of available food in FYM and slurry treated plots. In the spring and early summer of 1978 the activity of earthworms was low because of adverse climatic conditions, but during July to October activity was very high (Andersen in press). In control this caused a drop in biomass recorded in October 1978 compared to October 1977. At 50 to 200 tons/ha biomass was increased, although the number was lower. At 400 tons/ha there seems to be a long term effect of this large amount of manure. In October 1978 there is a considerable increase in number as well as in biomass. This is mainly caused by a very large hatching of new individuals of *A. caliginosa* and likewise an increase in the number of adult individuals, especially in FYM.

The general impression is that FYM favours more balanced proportions of the individual species than does slurry. The reason for this must be that FYM satisfies the food requirements of a greater number of species as compared to slurry, which also has a direct negative effect on deepburrowing species. The edaphic and biological significance of these findings is that a greater number of deepburrowing species as found by FYM treatment favours water infiltration rates (Baeumer and Bakermans, 1973), gas exchange and deep rot penetration. These soil properties are of great value for the crop during both heavy rain and periods of drought.

QUESTIONS and COMMENTS

E.F. NEUHAUSER: Please differentiate between slurry and farmyard manure.

C. ANDERSEN: Slurry is a mixture of urine and faeces, generally encountered in intensive cattle and pig management. The slurry is stored in barrels in a liquid state as opposed to farmyard manure which is in a semi-solid state also containing a certain amount of straw.

S. HILL: Have you looked, or do you intend to look, at the effects of composting manures or their effects on earthworms?

C. ANDERSEN: This has not been studied by us.

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EFFECTS OF HEAVY PIG SLURRY CONTAMINATION ON EARTHWORMS IN GRASSLAND

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INTRODUCTION

Animal manures applied to grassland on various soil types as semi-liquid slurry, have shown no significant ill effects on earthworms when spread at rates related to sward nutrient requirements and transitory detrimental effects when these rates exceeded sward nutrient requirements by an order of magnitude (Curry, 1976; Cotton and Curry, 1979a, b).

This paper reports on some effects of gross contamination, arising from the disposal of large quantities of pig slurry over a period of several years, on earthworm populations. Pig slurry can contain up to 700 ppm (dw) of copper resulting from the addition of 200 ppm copper as sulphate salt to pig feed (McGrath et al., 1977). Accordingly, particular attention was given to the possibility of toxicity to earthworms from this source.

EARTHWORM POPULATIONS

An abandoned quarry in an old pasture field at Celbridge, Co. Kildare, had been used for disposing of large quantities of pig sluury for 6 - 7 years until just over one year prior to our first earthworm sampling. The quarry was located on a 25° slope and in wet weather the slurry periodically overflowed, heavily contaminating the pasture downhill. The last major overflow prior to earthworm sampling occurred in the Spring of 1977.

In April and November 1978 earthworms were sampled by the formalin method at intervals along a gradient from the quarry lip to 75 m downhill. Soil and earthworm samples from each sampling station were retained for copper analysis by atomic absorption spectrophotometry. Earthworms were held for 3 das to permit expulsion of soil from the gut prior to analysis.

Earthworms were virtually absent from soil in the immediate vicinity of the quarry in April (Figure 1) but populations reached a density comparable with that in adjacent uncontaminated pasture at about 60 m downhill from the quarry. Biomass data exhibited almost identical trends (Figure 2). Table 1 gives the species composition of the fauna in April. In heavily contaminated soil adjacent to the quarry the compost worm, Eisenia foetida, was virtually the only species present. And the surface, organic matter feeding species, Satchellius mammalis

○ Nov 78 □ April 78 ■ Soil (April 78)
¹ Adjacent uncontaminated area ² Edge of contaminated area

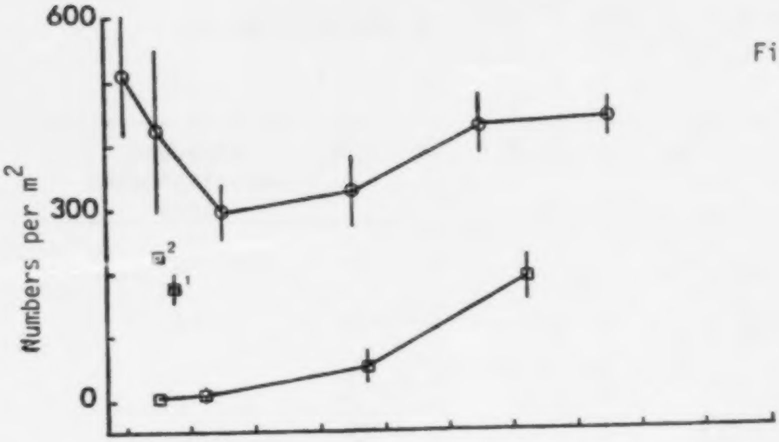

Fig. 1. Density of earthworms. Mean nos. at each sampling station with standard errors

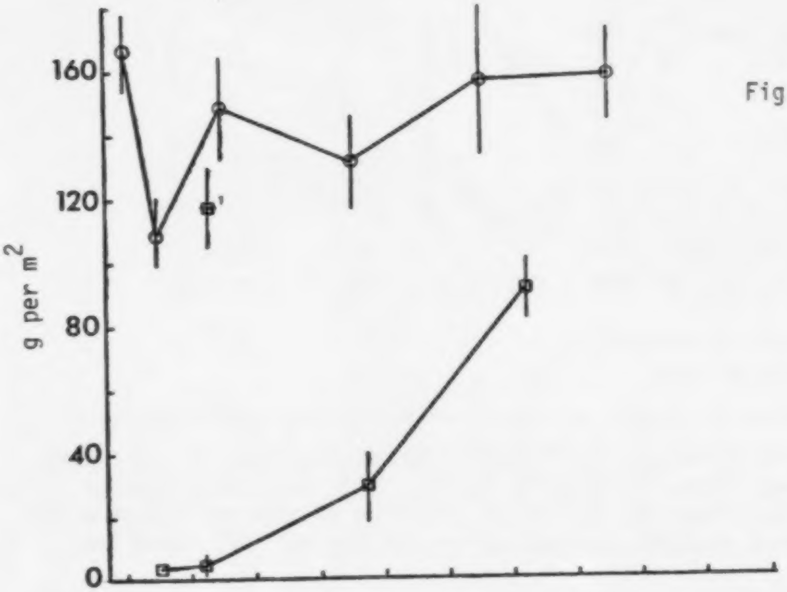

Fig. 2. Mean biomass of earthworms with standard errors

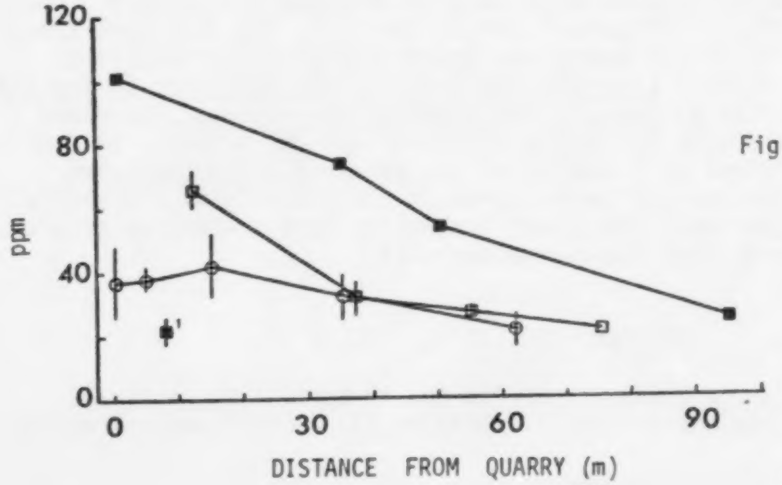

Fig. 3. Mean copper levels with standard errors

TABLE 1. Earthworm density (Nos m^{-2}) at increasing distances from the quarry in April, 1978.

	5m	5m*	12m	37m	62m	Adjacent uncontaminated area
Allolobophora chlorotica (Sav.)			1	7	69	30
Aporrectodea caliginosa (Sav.)		4		4	10	14
A. rosea (Sav.)		4		2	2	1
A. longa (Ude)					2	2
Allolobophora/Aporrectodea (immatures)		4		10	23	63
Satchellius mammalis (Sav.)		80		9	16	3
Eisenia foetida (Sav.)	2	28	13	2	2	2
Lumbricus terrestris L.		8		3	3	12
L. festivus (Sav.)		4		1	7	
L. castaneus (Sav.)		80		1		2
L. rubellus Hoff.				4	27	2
Lumbricus immatures		16		8	30	54
Total	2	228	14	51	191	185

*at edge of contaminated area

and *Lumbricus* spp. were present in higher proportions along the gradient than in the field away from the organic spill. This was particularly true of one sample 5 m from the quarry at the edge of the spill where the fauna appeared to have escaped decimation by the Spring 1977 overflow.

By November population density and biomass had reached high levels, particularly at the quarry edge where density exceeded 500 worms/m^{-2} and biomass exceeded 160g m^{-2} (Figures 1 and 2, Table 2). At this time the fauna in the vicinity of the quarry was dominated by surface dwelling pigmented species, notably *Lumbricus festivus*, *L. castaneus* and *E. foetida*. These species, and also *S. mammalis* and *Dendrodrilus rubidus*, decreased noticeably in numbers with increasing distance from the quarry. By contrast, typical grassland soil species of the genera *Allolobophora* and *Aporrectodea* were considerably more scarce in the vicinity of the quarry than they were farther down the slope, suggesting that these species are much slower to recover from the slurry toxicity.

COPPER TOXICITY

Results of copper analysis carried out in April 1978 confirmed the presence of a gradient in the soil (Figure 3). Copper concentrations

TABLE 2. Earthworm density (Nos m^{-2}) at increasing distances downhill from the quarry in November, 1978.

	0m	5m	15m	35m	55m	75m
Allolobophora chlorotica (Sav.)	38	22	29	74	130	82
Aporrectodea caliginosa (Sav.)	2	3	17	24	23	29
A. rosea (Sav.)	1			3		11
A. longa (Sav.)		1	2	3	4	4
Allolobophora/*Aporrectodea* immatures	16	16	38	54	61	132
Satchellius mammalis (Sav.)	26	26	7	7	8	39
Dendrodrilus rubidus (Sav.)	30	26	12			
Dendrodrilus immatures	15	24	5	7	12	4
Eisenia foetida (Sav.)	65	42	14		4	
Lumbricus terrestris L.		1	2	17	8	14
L. festivus (Sav.)	61	32	50	17	38	4
L. castaneus (Sav.)	82	42	14	10	15	18
L. rubellus Hoff.	19	26	62	17	8	11
Lumbricus immatures	155	155	34	94	119	82
Lumbricus eiseni Lev.	3	6				
Eiseniella tetraedra (Friend)	1					
Octolasion cyaneum (Sav.)						7
Octolasion immatures			5			
Total	514	422	291	327	430	437

in earthworms in April paralleled this gradient, the highest levels (82.5 ppm) recorded being in specimens of *Lumbricus terrestris* from about 10 m below the quarry lip. A less pronounced gradient in earthworm copper levels was recorded in November although a strong negative correlation between copper levels and distance from the quarry was in fact recorded ($r = -0.93$).

There is evidence to suggest that levels of soil copper comparable to those occurring adjacent to the quarry can be extremely toxic to earthworms (Nielson, 1951; van Rhee, 1977). Accordingly, further field sampling and some laboratory tests were carried out to assess relationships between pig slurry and possible copper toxicity to earthworms. Table 3 gives data for two contrasting situations. Clearly, short-term applications of pig slurry at high levels have little influence on soil or earthworm copper levels. Long-term dumping at Celbridge resulted in a very significant elevation of soil copper and a much less pronounced elevation in earthworm bodies. The copper content of the earthworm faeces (460 ppm) reflected very closely that of the soil.

TABLE 3. Levels of copper (ppm) in earthworms from soils contaminated by pig slurry.

Site	Contaminated Soil	Earthworms from Contaminated Soil	Earthworms from Uncontaminated Soil
1. Celbridge, Co., Kildare, abandoned quarry where large amounts of slurry were dumped 1960-71.	483	53.6 ± 10.5	16.3
2. Johnstown Castle, Co., Wexford, sandy loam grassland soil which received 690 m^3 ha slurry during 1976-77	20	18.5	17.5

Earthworms were cultured in two old pig slurry composts obtained from disposal sites at Celbridge and containing respectively 101 and 483 ppm copper. Worms of mixed species composition from local grassland were used, six worms being added to each 1 kg glass culture jar. Figure 4 indicates survival in the two culture series and Figure 5 shows how copper levels in survivors varied with time. Survival trends were fairly similar in both types of slurry until the third month when much greater mortality was evident in the high-copper slurry. Thereafter, the trends were fairly similar with approximately 30% survival until the seventh month. Trends in earthworm copper levels remaining fairly constant at 30 to 50 ppm in the "low copper" slurry whereas levels increased quite dramatically in the "high copper" slurry, reaching 200 ppm after 5 months.

DISCUSSION

The study confirms that gross pig slurry pollution of grassland is extremely toxic to earthworms in the short term. Test introductions indicate that the slurry is no longer toxic to the coprophilous species _E. foetida_ after 4 wk but considerably longer is required for significant natural recolonization to occur. It appears to take 12 to 18 mo for populations to recover to pre-contamination levels and probably considerably longer for many true soil-feeding grassland species.

The likely effects of high soil copper levels arising from pig slurry on earthworm numbers are problematical. Mitchell et al. (1978)

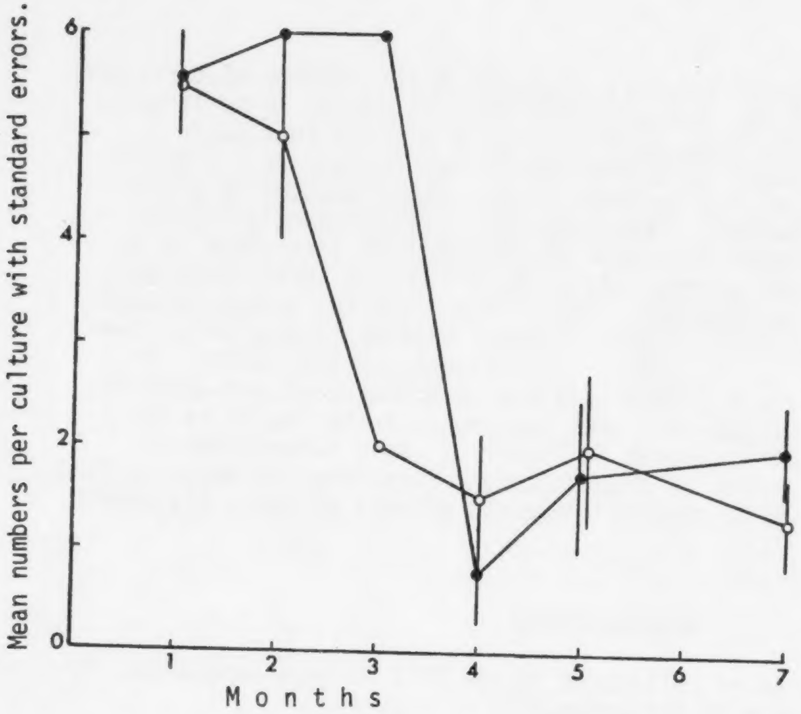

Fig. 4. Survival of earthworms in slurry containing 101 ppm (—●—) and 483 ppm (—○—) copper.

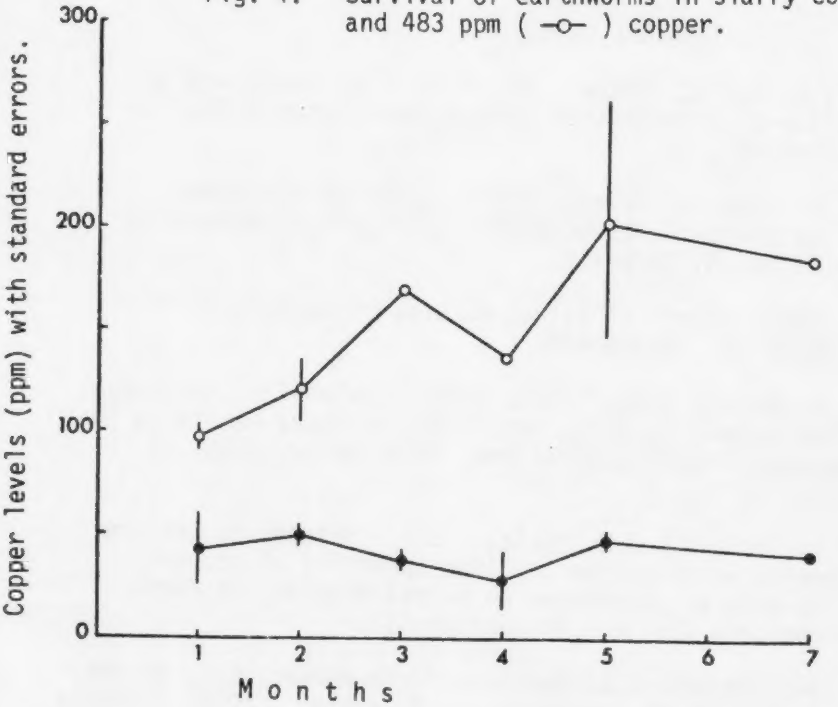

Fig. 5. Mean copper levels in earthworms in slurry containing 101ppm (—●—) and 483ppm (—○—) copper.

reported thriving populations of E. foetida in soil-sludge mixtures containing up to 253 ppm Cu, most of which they considered to be largely immobile. On the other hand, present results suggest that toxic copper doses can be acquired by earthworms from pig slurry. A difficulty arises in determining how much of the copper present in slurry is available to earthworms. Slurry copper is predominantly tightly complexted in organometal form with minimal amounts (less than 3% in the present case) being acetic acid soluble. Copper levels recorded in earthworm faeces suggest that most of this material passes through the gut unabsorbed, but yet levels recorded from earthworm bodies cannot be accounted for by the acetic acid soluble fraction alone. It appears likely that further fractions may be decomplexed and absorbed during passage through the gut, thus leading to mortality or to the kind of accumulation illustrated in Figure 5. More information is needed on the availability of organic copper to earthworms before a full assessment can be made of the environmental effects of heavy pig slurry contamination.

ACKNOWLEDGMENT

We are indebted to colleagues in the Soil Science Department for advice and assistance with the estimation of copper.

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QUESTIONS and COMMENTS

M.S. GHILAROV: Why is the copper content in pig slurry so high?

J.P. CURRY: Because of the practice of adding 200 ppm of copper as sulphate salt as a growth promoting substance in pig diets.

S.B. HILL: I feel that we should be cautious to conclude that the repeated addition of non-biodegradable, potentially toxic materials, such as copper, to soils do not pose a problem. Surely the only outcome can be a gradual increase in the concentrations of such materials (or their dissipation into adjacent environments where they may also have negative effects) and the eventual reaching of threshold levels at which negative effects are experienced. The fact that copper is initially unavailable may not be permanent. Critical thresholds may be reached, for example, following a change in soil management practices. (Just as chlorinated hydrocarbons stored in our own fat tissues are harmless until we decide to lose weight!)

J.P. CURRY: I agree,and indeed I am unhappy about the assumption that seems to be frequently made that heavy metals in organic wastes are largely unavailable and do not therefore constitute an environmental hazard.

M. HASSALL: Do you know in which tissues of the earthworm the copper is accumulated?

Do you know how efficiently the earthworms are at excreting this copper load when returned to a copper free diet?

J.P. CURRY: No, nor have I been able to find any information in the literature on this point.

No, in answer to your second question.

H. EIJSACKERS: Did you notice any avoidance of the contaminated soil by the earthworms?

J.P. CURRY: No. We have observed that earthworms exposed to heavy slurry contamination are killed very quickly and we do not consider that they would be able to move out of the affected area quickly enough to avoid the effects of a major overflow.

EARTHWORMS AS BIOLOGICAL MONITORS OF CHANGES IN HEAVY METAL LEVELS IN AN AGRICULTURAL SOIL IN BRITISH COLUMBIA

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ABSTRACT

Individuals of Lumbricus rubellus and Allolobophora chlorotica were sampled from an agricultural soil on Westham Island, British Columbia, Canada. Earthworms, their faeces and soil were analyzed for cadmium, copper, lead and zinc. Cadmium and Zn were concentrated by all species over the soil levels while copper and lead were not. Mature adults of L. rubellus had higher levels of Cd than had immature adults.

In the laboratory, sewage sludge with high levels of the above heavy metals was added at different rates to the soil. The effects of the treatments on the concentrations of heavy metals in earthworm tissue and faeces were examined. Of the metals, cadmium levels in the earthworms increased until soil levels exceeded 6 ppm.

INTRODUCTION

Various species of earthworms have been found to concentrate certain heavy metals, both in soils which had low levels of metals and in soils which were contaminated and so had high levels (see review in Edwards and Lofty, 1977). In recent studies, cadmium was concentrated by the compost worm, Eisinia foetida Savigny and cadmium, nickel and zinc were accumulated by individuals of this species when sewage sludge was amended with various amounts of salts of these metals (Hartenstein et al., in press). In Copenhagen, Denmark, Andersen (in press) found that several species of earthworms concentrated cadmium, but not lead, over soil levels. In the United States, a particular earthworm species studied by Helmke et al. (1979) concentrated Cd, cobalt, mercury and Zn. Their field study on the effects of sewage sludge application on heavy metal levels in earthworms showed that Cd, Zn and Cu levels in earthworm tissue increased as sludge application rates increased.

Earthworms have been shown to be important in redistribution of Cd, carbon and cesium in soils in the southeastern United States (Oak Ridge National Laboratory, 1974). The introduction of European species to New Zealand pastures has greatly increased the amounts of molybdenum available for plants (Edwards and Lofty, 1977). The Oak Ridge report, referred to above, included data from radiotracer experiments. Such work needs to be done in concert with investigations of levels of stable isotopes of heavy metals in earthworms and their food. However, for a thorough evaluation of the role of earthworms in heavy metal redistribution by their burrowing, feeding and excretory activities, data on possible variation in soil according to depth and the corresponding levels in tissue and faeces of earthworms in relation to age, species of worm and seasonal activity are required. Ireland and associates studied variation within earthworm species according to season and also variation between species. Lead levels were highest in the winter months (Ireland and Wooton, 1976) and Pb and Zn concentrations varied between the two species examined.

The objective of this study was to determine if earthworms could be used to monitor levels of heavy metals in a particular soil. To investigate this we compared the levels of cadmium, copper, lead and zinc in soil collected from Westham Island, British Columbia and in the tissue and faeces of different species of earthworm living in that soil. In the laboratory, the effects of applications of sewage sludge, with high levels of the above metals, on the concentrations in soil and earthworms were then investigated.

METHODS

Random samples of earthworm populations in a clover field on Westham Island, British Columbia were taken along line transects in September and November 1978 and in April 1979. Worms were washed with distilled water and individually placed in plastic Petri dishes with moistened ashless filter paper for six days and kept at 15 C. Faeces were collected daily. Earthworms and faeces were dried at 65 C for four days and then weighed on a microbalance.

The sample preparation method for earthworm tissue and faeces depended on sample size. Earthworm samples of between 10 and 120 mg dry weight and faecal samples of between 10 and 75 mg dry weight were acid digested in small glass tubes while earthworms and faeces heavier than the above weights were acid digested in glass beakers. The latter method was also used for soil samples of approximately 250 mg dry weight.

The first method is a modification of that described by Koirtyohann et al. (1976). Oven-dried samples were weighed into glass vials (Kimax 70 x 20 mm O.D.) and solubilized with concentrated HNO_3 and 30% H_2O_2 using a block digestor set at 150 C.

The method for larger samples was modified from Van Loon and Lichwa (1973). Samples were digested with concentrated HNO_3 in 100 ml glass beakers heated on a hot plate. All glass and plastic containers were washed in 8N HNO_3, and water used for all dilutions and rinses was distilled in glass and deionized.

Analysis of Zn, Cd, Pb and Cu was done using a Perkin-Elmer Model 306 atomic absorption spectrophotometer equipped with an HGA-2100 graphite furnace and deuterium arc background compensation. Most samples contained sufficient Zn (>0.5 ppm) for flame analysis. Cadmium, Cu and Pb analyses were done using the HGA-2100. Twenty μl injections were made two or three times from each sample. In all runs, NBS orchard leaves and bovine liver and soil standards were used to check for accuracy. Also, an internal worm standard was made up of earthworms whose guts had been voided prior to killing, drying and thorough grinding. Standards were prepared in 0.16N HNO_3.

RESULTS

Cadmium and Zn were concentrated by all earthworms over the soil levels, and the low levels of these elements in the faeces (Table 1) reflected their high assimilation by the earthworms. Mature adults of Lumbricus rubellus had higher levels of cadmium than had immatures (Figure 1 and Table 1).

Copper and Pb levels in earthworm tissues were low in comparison with soil levels.

Mature adults of L. rubellus were used in the sewage sludge experiments. The effects of sludge applications on cadmium and copper levels in the soil and in the tissue and faeces of this earthworm are shown in Figure 2 and in Figures 3 and 4 respectively.

Cadmium concentrations in earthworm tissue increased steadily as soil levels increased to approximately 6 ppm after which concentrations in the former appeared to level off. Concentrations in the faeces initially increased but levelled off after soil levels exceeded 2.4 ppm.

In contrast, Cu concentrations in earthworm tissue and faeces were not much affected by sewage sludge applications. Variances around the mean levels, in both these substrates were wide but concentrations were consistently higher in the faeces (Figure 4).

DISCUSSION

Soils with low levels of metals

Data from other studies are compared with those from this study in Table 2. Where possible, we have indicated whether the earthworm samples analyzed included mature adults or immature adults or both. In all cases, Cd was concentrated by earthworms and the levels in faeces were low. Lowest levels of Cd were found in samples of mixed genera of various age groups (see, for example, control data of Gish and Christensen, Table 2). These low levels may have been due to pooling of some earthworm species or age groups of low Cd levels with other species or age groups of high levels. In this regard, the low concentrations of Cd for immature adults of Lumbricus rubellus found in our study suggests that there may be variation between different age groups of this species in other parts of its geographical range and between age groups of other species also.

Low Cu levels occurred in both tissue and in faeces of earthworms collected from soils with low levels. Lead levels in earthworms in our

TABLE I. LEVELS OF HEAVY METALS IN TISSUES AND FAECES OF EARTHWORMS COLLECTED FROM WESTHAM ISLAND, BRITISH COLUMBIA

	ppm DRY WEIGHT ± SD							
	CADMIUM		COPPER		ZINC		LEAD	
	TISSUE	FAECES	TISSUE	FAECES	TISSUE	FAECES	TISSUE	FAECES
Lumbricus rubellus								
Mature Adults	10 ± 3.0 (19)	0.3 ± 0.10 (15)	10 ± 3.0 (8)	30 ± 2.7 (17)	260 ± 40 (13)	50 ± 13 (15)	0.30 ± 0.10 (5)	-
Immature Adults	4 ± 1.0 (19)	0.2 ± 0.03 (9)	13 ± 4.0 (5)	24 ± 6.0 (10)	270 ± 30 (19)	35 ± 7 (19)	-	
Allolobophora chlorotica	8 ± 2.4 (13)	0.3 ± 0.10 (5)	8 ± 2.4 (9)	25 ± 4.9 (5)	210 ± 45 (14)	-	0.60 ± 0.50 (9)	-

Number of samples in parentheses

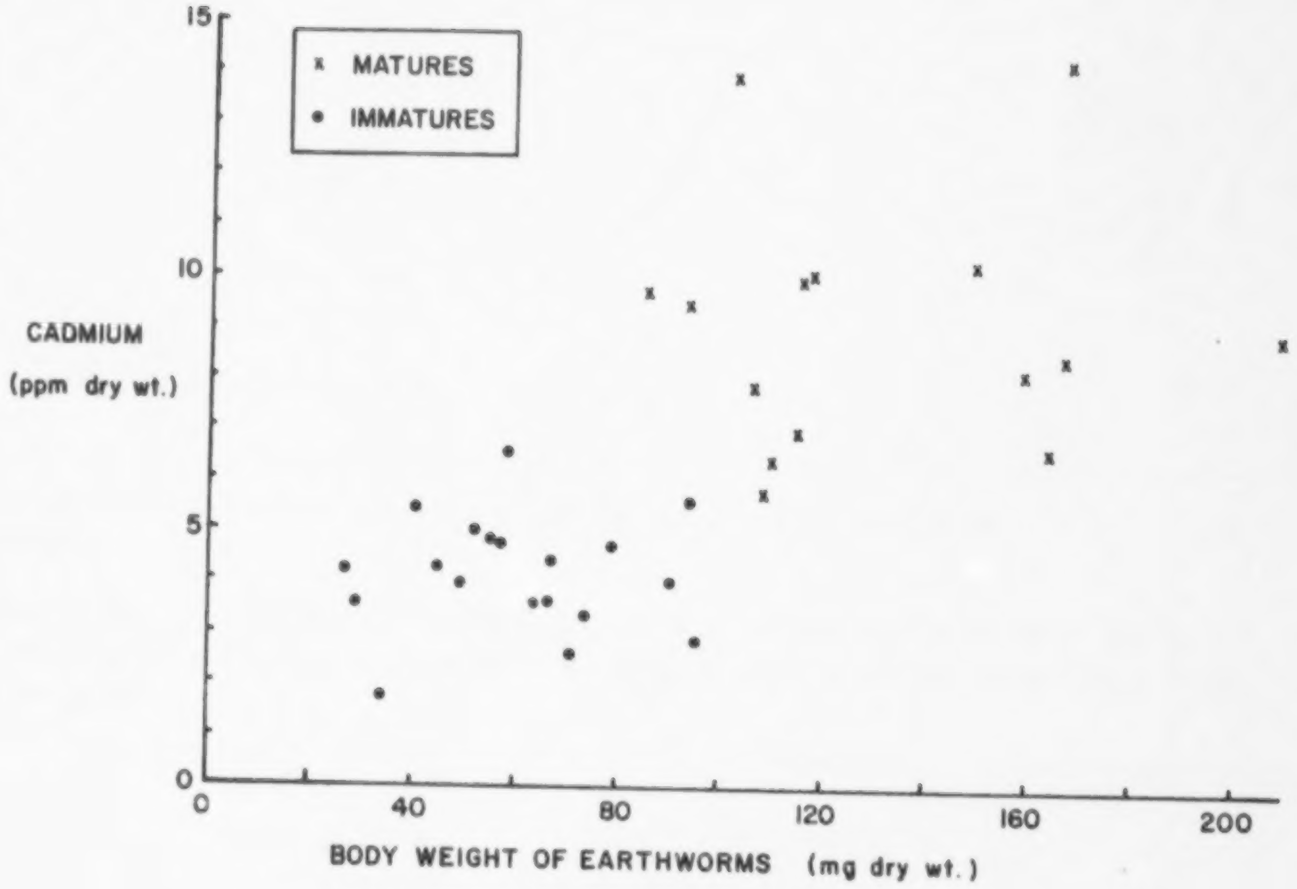


Figure 1. Cadmium levels in immature and mature adults of Lumbricus rubellus

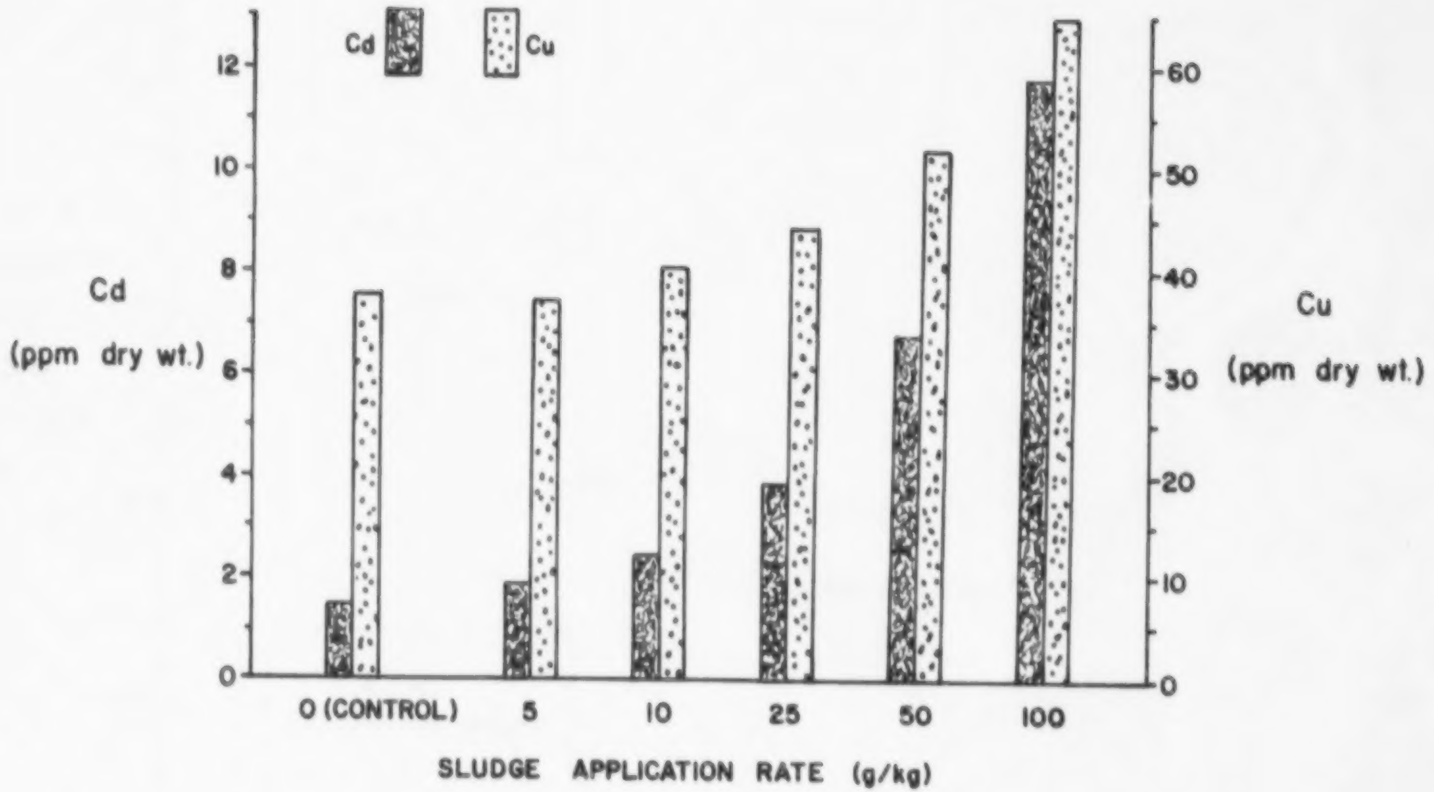


Figure 2. Effects of various application rates of sewage sludge on heavy metal levels in soil.

Figure 3. Effects of sewage sludge applications on cadmium levels in tissue and faeces of mature adults of Lumbricus rubellus.

Rates of sludge application (g/kg air dried soil) in parentheses.

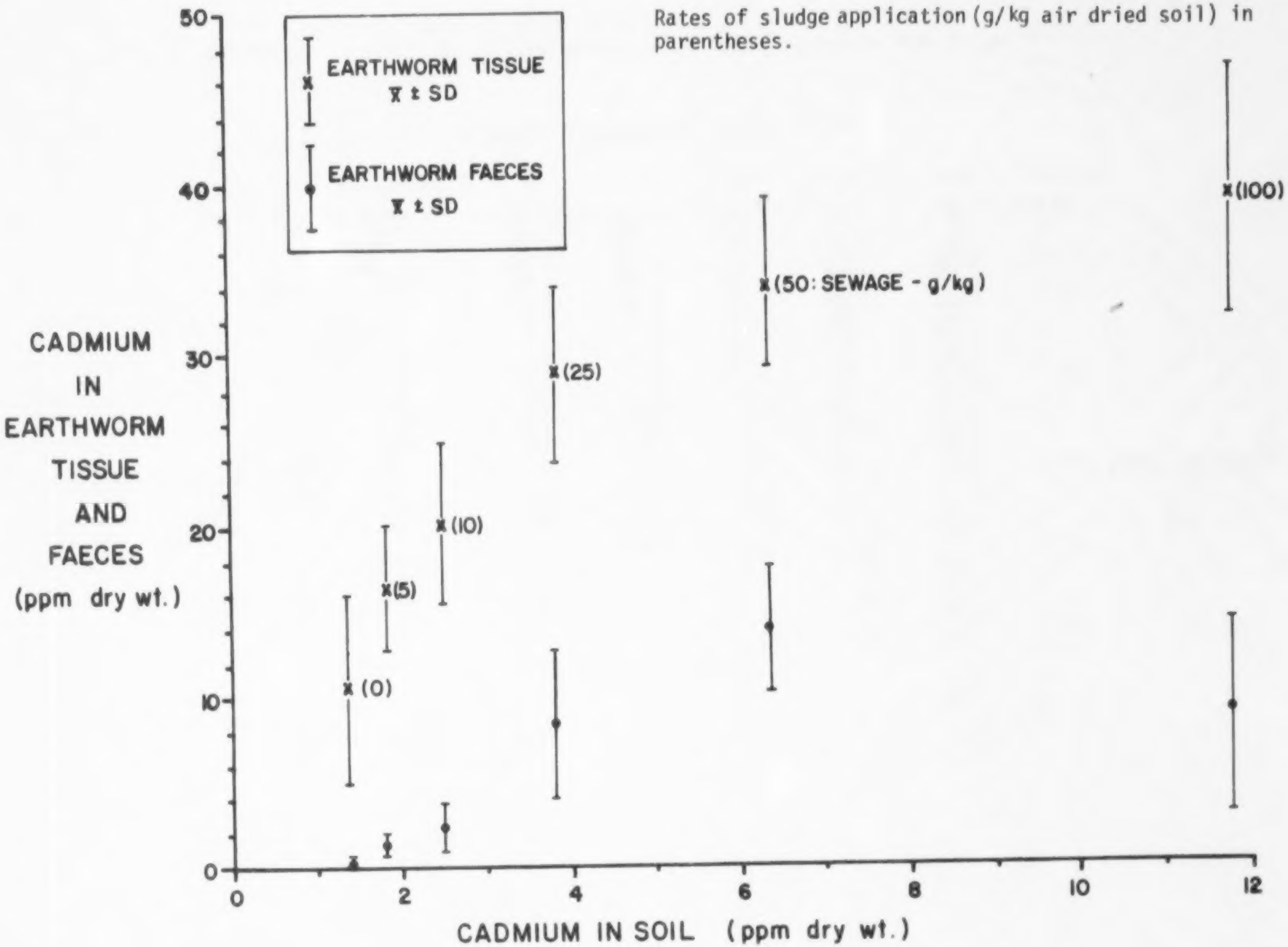
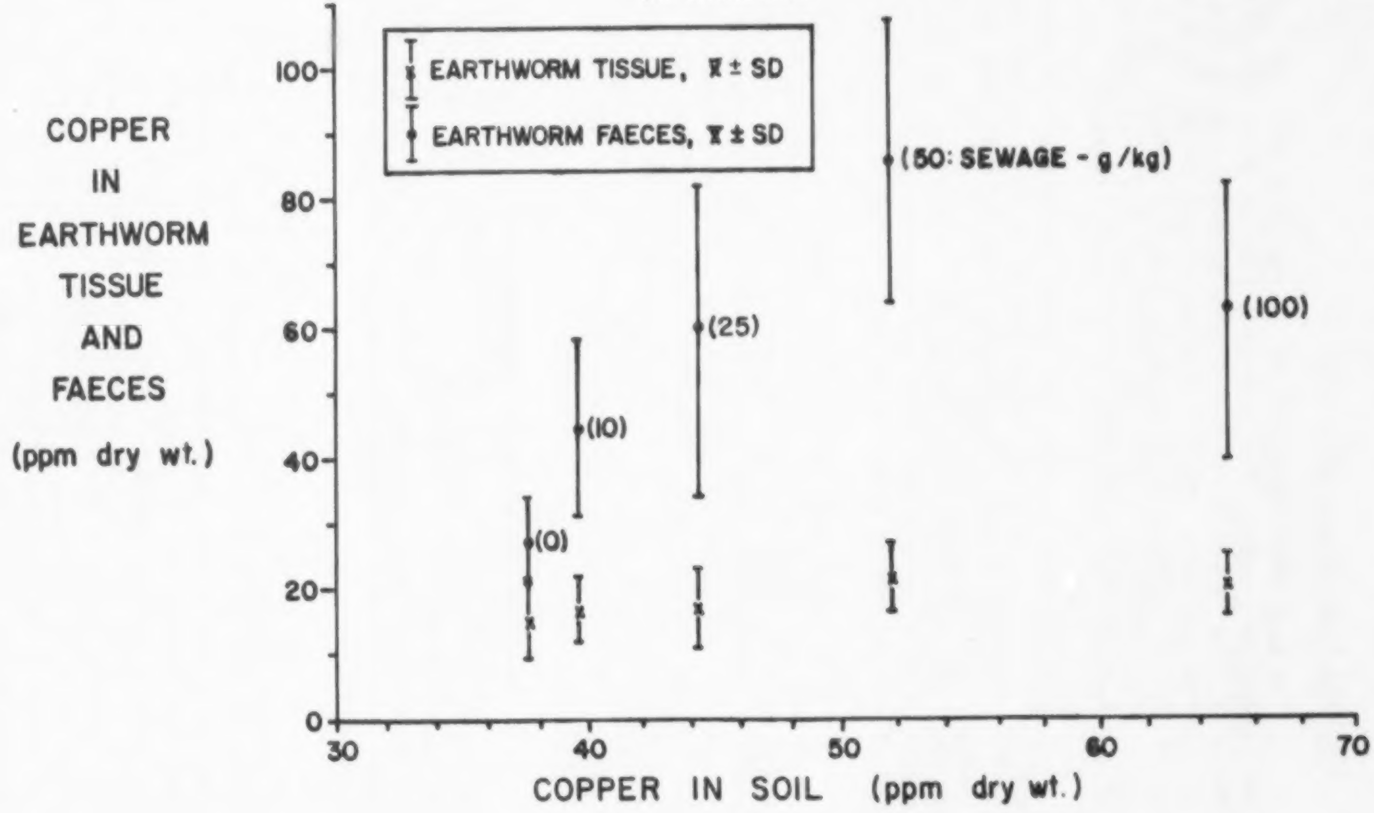


Figure 4. Effects of sewage sludge applications on copper levels in tissue and faeces of mature adults of Lumbricus rubellus.

Rates of sludge application (g/kg air dried soil) in parentheses.



study and in other studies were also low (Table 2). In all studies, Zn was found to be concentrated by earthworms. Levels in faeces were uniformly low.

Soils with high levels of metals

The very high levels of Pb in the acid tolerant *Lumbricus rubellus* and *Dendrobaena rubida* from a mining area in Wales are striking. This is the only case in which Pb is reported as having being concentrated by earthworms over soil levels. The low levels of Pb in these species collected by Ireland and associates from the control site were still higher than those reported in this present study and elsewhere and reflect a rather high Pb level (150 ppm) in the soil (Table 2).

Several studies have focused on the effects of sewage sludge application rates on heavy metal levels in soil and earthworms. Other studies have considered the effects of pollutants from automobiles,while that of Van Rhee (1977) looked at the effect of pig slurry, high in Cu, on the levels in soils and earthworms. These studies and our study on sewage sludge applications will now be considered so as to evaluate the use of earthworms as monitors of heavy metal levels in soils.

Gish and Christensen (1973) found that samples of mixed genera of earthworms accumulated Cd, Pb and Zn over the levels in soil adjacent to highways with heavy automobile traffic. Some of their data are included in Table 2. Concentrations of Cd, Pb and Zn in both earthworm tissue and soil decreased significantly with increasing distance from the highways. Thus, earthworms could be used to monitor levels of these metals in this soil. In relation to Cu, Van Rhee (1977) found a significant correlation between Cu levels in soils and in earthworm tissue in pastures contaminated in pig slurry. In this case, Cu levels in worms reflected increases in soil levels.

Data from the sewage sludge application experiments are more difficult to evaluate. This is particularly so for field studies; those of Helmke et al. (1979), Hartenstein et al. (in press) and Andersen (in press). In such studies, it is difficult to sample sufficient numbers of earthworms for good statistical analyses,and in long term studies possible variation in heavy metal levels in earthworms according to age and season should be considered.

In our laboratory study, cadmium levels in mature adults of *Lumbricus rubellus* increased steadily until the soil levels exceeded 6 ppm. Moreover, the Cd levels in the faeces of these earthworms did not change when soil levels were approximately 4 ppm and greater. These data suggest that the feeding and excretory activities of the worms slowed down. This may have occurred because of toxic effects of high Cd levels (and perhaps those of other metals such as Ni) at the higher sludge application rates. Such effects would be more pronounced in studies carried out in laboratory containers, as ours was. In the field, sludge-amended soil under the influence of natural weather conditions would likely undergo more extensive physiochemical and biological changes. This would affect the availability of metals to earthworms. De Vries and Tiller (1978) showed that glasshouse

TABLE II. LEVELS OF HEAVY METALS IN EARTHWORMS AND SOILS FROM VARIOUS STUDIES

TAXON	ppm DRY WEIGHT CADMIUM	COPPER	LEAD	ZINC	COMMENTS	REFERENCE
Apporectodea tuberculata						
Tissue (M)	13.7	9.2	-	260	From Control Areas	Helmke et al. (1979)
Faeces (M)	0.55	10.6	-	60		
Soil	< 0.5	-	-	100		
Apporectodea trapezoides						
Tissue (M)	8.4	10.5	1	380		E.A. Kenney (unpublished)
Faeces (M)	0.3	32	14	60		
Allobophora chlorotica						Present Study
Tissue (M + I)	7.5	7.5	0.60	210		
Faeces (M + I)	0.30	25	-	-		
Lumbricus rubellus						
Tissue (M)	10	10	0.30	260		
Faeces (M)	0.30	30	-	50		
Tissue (I)	4	13	-	270		
Faeces (I)	0.30	24	-	35		
Soil	1.4	37	15	110		
Eisinia foetida						
Tissue	8 - 46	20 - 150	1 - 53	68 - 210		Hartenstein et al. (in press)
Sludge	12 - 27	380 - 610	160 - 900	875 - 2100		
L. rubellus	-	13	3590	740	Heavy Polluted	Ireland and Richards (1977)
Dendrobrena rubida	-	17	7590	310		
Soil	-		1960	880	Cwmystwyth Site	and
L. Rubellus						
Tissue	-	15	25	650	Control Site	Ireland and Wooton (1976)
D. Rubida						
Tissue	-	15	37	250		
Soil	-	2	150	170		

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TABLE II. CONTINUED

TAXON	ppm DRY WEIGHT CADMIUM	COPPER	LEAD	ZINC	COMMENTS	REFERENCE
Allolobophora longa						Andersen (in press)
Tissue	5.7	-	4.6	-		
Faeces	0.53	-	45.0	-		
Soil & Sewage Sludge	0.65	-	28	-		
Tissue	9.2	-	5.9	-		
Faeces	1.60	-	105	-		
Soil & Sewage Sludge	0.99	-	39	-		
Lumbricus terrestris Tissue	14	-	14	-	From Near Major Street	Andersen (in press)
Soil	0.65	-	140	-		
Mixed Genera Tissue	5.7	-	4.7	320	Mean of 6 Sites	Van Hook (1974)
Soil	0.37	-	27	43		
					Distance from Major Highways	
Mixed Genera Tissue (M + I)	12.6	-	270	560	10 m	Gish and Christensen (1973)
Soil	1.23	-	468	180		
Tissue (M + I)	8.8	-	113	400	20 m	
Soil	0.72	-	136	75		
Tissue (M + I)	8.3	-	81	410	40 m	
Soil	0.72	-	71	64		
Tissue (M + I)	6.9	-	44	320	80 m	
Soil	0.68	-	48	52		
Tissue (M + I)	7.1	-	53	240	180 m	
Soil	0.72	-	53	60		
Tissue (M + I)	3.0	-	12	220	Control	
Soil	0.66	-	14	42		
Mixed Genera Tissue	-	41	-	-	Samples From Mean of 9 Sites	Van Rhee (1977)
Soil	-	24	-	-		

M and I refers to mature adults and immature adults, respectively.

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experiments, even with large pots, can give completely erroneous indications of the probable uptake of heavy metals by vegetables in sludge-treated soils under field conditions. Also, the sludge and soil used in our experiments were thoroughly mixed. In field experiments, sludge would not be so well incorporated with soil and there would certainly be more heterogeneity in soil levels of heavy metals. Earthworms might then disperse from local areas of high Cd levels or might selectively feed on soil of lower Cd concentrations.

Our study and other studies indicate that earthworms of various species can be used to monitor levels of cadmium in soil and, under certain conditions, copper levels in earthworms reflect soil concentrations. Further work is required to be done on the uptake of cadmium by earthworms from soils with high levels. Such investigations should also be carried out in mini-field plots.

ACKNOWLEDGEMENTS

We thank L.M. Lavkulich for critical comments and B. von Spindler for technical assistance with the Graphite Furnace. L.E. Lowe provided soil standards. The study was financed by the Natural, Applied and Health Sciences Grants Committee (The University of British Columbia), National Sciences and Engineering Research Council of Canada (67-6177) and Agriculture Canada (65-0360) grants.

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QUESTIONS and COMMENTS

M. GORNY: May you explain why the earthworms are living in good condition and high density in such environments as grasses near to roads, fields treated with slurry, where there is a great deal of heavy metals?

A. CARTER: Earthworms living near busy highways and in other polluted environments may suffer sub-lethal effects of heavy metal poisoning. In our study, the levelling off of Cd levels in earthworm tissue without a concomitant increase in faecal levels may have been due to the high Cd levels in the soil having toxic effects. Thus, these high levels could have slowed down the feeding and excretory activities of the worms.

P. BERTHET: Do you have any information concerning the localization of the cadmium in the worm's body? What are the physiological implications of cadmium accumulation?

A. CARTER: Cadmium (unlike lead) has not been found to be localized in earthworm tissue. Most of the work on the physiological effects of Cd accumulation has been done with mammals. Cadmium may have marked effects on copper and, to a lesser extent, on zinc metabolism. Antagonism of the former metal by Cd could have a secondary effect on haemoglobin biosynthesis.

C.A. EDWARDS: Did you do any studies of excretion of heavy metals from earthworms in clear soil?

A. CARTER: No.

INFLUENCE OF TRAMPLING OF A HORSE MANADE IN CAMARGUE ON THE SOIL FAUNA AND THE FAUNA OF CANOPY

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INTRODUCTION

The trampling impact of a manade (a group of half-wild horses) was the subject of this research. This herd was composed of seven mares from four different breedings, yearlings and a stallion (during the period of reproduction). The manade roamed over a 120 ha area in Camarque, which was dominated vegatively by *Salicornictum fruticosae*. The authors while studying the feeding behavior of *these breeding horses of* Carmarque, observed that they graze mainly on the salt and reed marshes and in the *Saticornia fruticosa* formations. Our research, therefore, was concentrated on the latter habitat type in which two experimental areas were established.

METHODS

Two square quadrats (24 x 24 m) were delimited within the homogenous area of the *Salicornia fruticosa* association (known also as Sansouire). Samples of the pedofauna(oligochaetes and arthropods) and a canopy fauna were collected monthly from the four smaller squares (each 4 m on a side) each within a grazed and a test (control) quadrat. The fauna were represented by a few cosmopolitan species.

RESULTS

Comparative Community Structures

When specific diversity, maximal diversity and equitability of collembolan communities between the experimental sites were compared only a small difference in equitability was noted, however, it was non-significant (Table 1). Likewise, a comparison of these same animal global communities using Spearman rank correlation coefficients shows no significant difference in the communities. When the community structure for two periods were considered, the first sampling period and the last, we observed a change in equitability (Table 2).

Table 1: COMPARATIVE GLOBAL COMMUNITY STRUCTURE OF COLLEMBOLA AS AFFECTED BY TRAMPLING OF A MANADE

Community Quantification	Grazed Site	Test Site
Specific diversity $H = 3.32 (\mathrm{Log}\ Q - \frac{1}{Q} \Sigma qi - \log qi)$.	2.56 bits	2.49 bits
Maximal diversity H max	3.45 bits	3.45 bits
Equitability $\frac{H}{H}$ max x 100	73.99 %	71.96 %

Table 2: COMPARATIVE GLOBAL COMMUNITY STRUCTURE OF PEDOFAUNA (EXCEPT COLLEMBOLA) AS AFFECTED BY TRAMPLING BY A MANADE OVER TIME.

Community Quantification	Grazed Site		Test Site	
	First Sampling Period	Last Sampling Period	First Sampling Period	Last Sampling Period
H max	3.45	2.50	3.45	2.80
Equitability (%)	79.36	69.64	69.64	34.93

The decrease of equitability on the test site shows an increase of the heterogeneity of partitioning of individuals belonging to a single or a few species; the contrary occurred in the grazed station.

Concerning the pedofauna in general (except for the Collembola cited in Table 1) the values of equitability show the following: 1) the faunal composition of grazed and non-grazed sansouire is not significantly different considered annually, 2) the faunistic composition is not significantly different in the first series of samples but differs significantly among the last samples. We can then consider that by the end of a year there was a modification of pedofauna. Concerning canopy fauna, composition and structure were not significantly different.

Multivariate Analysis of Abundance

Multivariate analysis techniques were applied to the numerical abundance coefficients (Figure 1). At the microfaunal level (Collembola and Acarina), factor 1 neatly differentiates between the test and the grazed area (61% of the total inertia). The test area is positive, while the grazed area is negative. Factor 2 (28% of total inertia) divided Collembola from the acarines. The collembolan communities of the test area (Tclb) and those of the grazed site (sclb) are positive, whereas the mite communities of the test area (Tacr) and those of the grazed site (Sacr) were negative. Furthermore, factor 3 confirms factor 2. It always opposes Tclb and Tacr, and Sclb and Sacr, but with a reversal in relation to the first result. Factor 3 is more specific to the Collembola and opposes them more than it does the mites. This seems to indicate that Collembola have a different reaction than the one of the acarines to the introduction of the manade. On the contrary, there is little difference between Tacr and Sacr, concerning this factor.

The same analyses were applied to the canopy communities and the results confrim those above. No noticable differences appear between communities of the pedofauna of the test sansouire and grazed sansouire that permits a measure that can be related to the visable impact of the manade. On the other hand, canopy fauna had a similar structure and their dynamics only differed slightly in each biotope.

Finally, the pedofauna other than Collembola and Acarina manifests here again certain uniqueness; the distribution on factors 1 and 3 showed that in the grazed sansouire was individually scattered a way from the common nucleus of the species. For example, two sets were very distinct, the first formed by oligocheates and immature thomasids, and the second formed by an unknown spider and carabid larvae and the Coccidae. The scattering of these two aggregates in the grazed sansouire was caused by the frequentation of the manade.

Biomasses in this study were expressed uniformly as animal biomass/ vegetal biomass unit/monthly sample (each sample corresponding to six sample units). Variation in this biomass was negligible except for a decrease in the grazed sansouire during January and February and also in April and August.

DISCUSSION

Concerning the fauna and mainly the microfauna, the few studies that have been made regarding influence of trampling all point out a decrease of the number of representatives. In our study, we can only note a range of composition of pedofauna other than microfauna. In the reaction of those microfauna, particularly of the Collembola responding to the introduction of the manade, those insects were the first to react to the effects of trampling.

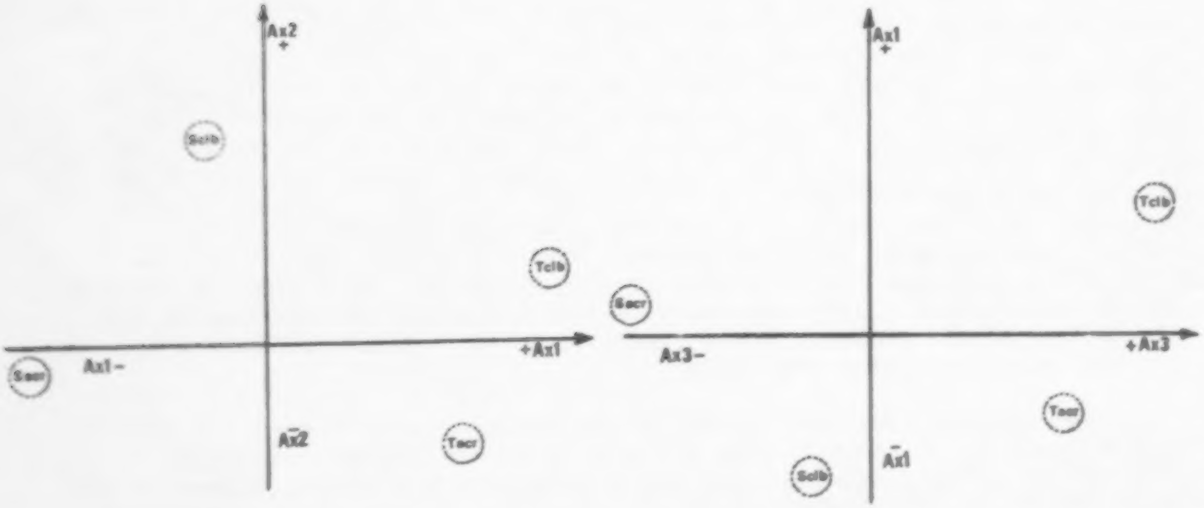

FIGURE 1 - Multivariate analysis - Distribution (in bimodal) of collembola and mites in test sansouire and in grazed sansouire.

SESSION V: INFLUENCE OF MINING SITE MODIFICATION AND REHABILITATION ON SOIL ORGANISMS

Moderator: Dennis Parkinson

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RESTORATION OF FUNGAL ACTIVITY IN TAILING SAND (OIL SANDS)

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Canada

INTRODUCTION

The Athabasca Oil Sands Deposit (c. 88% of the known Oil Sands in Alberta, Canada) contains more than 600 x 10^9 barrels of bitumen reserves. Consequently this area is subject to considerable natural resource development, with two major extraction plants currently in operation and several more in the planning phase.

In the two existing plants surface mining, involving stripping of vegetation and layers of clay, sand, gravel and boulders (up to 150 feet in thickness), is used to expose and remove the bitumen bearing sand. The extraction process involves the use of hot water, steam and caustic soda, and produces, as well as the desired bitumen, large volumes of an alkaline aqueous suspension of clays etc. and large amounts of sand. The aqueous suspension is stored in large tailings ponds which are dyked using the spent sand. It can be readily appreciated that this method of "waste disposal" creates severe problems for restoration of the land, and, consequently, in 1975 a comprehensive environmental research program was initiated to evaluate a range of aspects (air, land and water plus social impacts) of this industrial operation.

Until recently the major efforts in reclamation of the tailing sand centred round studies on plant species considered suitable for revegetation and on the effects of different types of surface amendment on survival and subsequent success of the chosen plant species.

Since it is abundantly clear that soil organisms play a vital role in organic matter decomposition and nutrient cycling, in 1977 a research program began to study the effects of different surface amendments on the restoration of biological activity in highly disturbed soils. This present contribution presents data obtained in this program on the initial (1-2 year) effects of different surface amendments on the redevelopment of biological activity in tailing sand from the Oil Sands.

EXPERIMENTAL PLAN

Large amounts of tailing sand were transported to Calgary and placed in a soil tank (54 x 10 m) to a depth of 1 m. The tank was constructed with internal dividing walls to allow three replicates of each of four different surface treatments. Four test plant species were chosen for growth in the tailing sand following application of the surface amendments.

Details on the amendments used and the plant species chosen are given in Table 1.

TABLE 1. Summary of amendments applied and plant species grown on tailing sand.

a. Plant species:

1. *Pinus banksiana* Lamb. (jack pine)
2. *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry)
3. *Agropyron trachycaulum* (Link) Malte (slender wheat)
4. *Onobrychis corniculatus* L. (sainfoin)

b. Amendments:

1. No amendment (control)
2. Fertilizer at level equivalent to 113.7 kg N, 113.7 kg P_2O_5 and 91.0 kg K_2O ha^{-1}
3. Sewage sludge at level equivalent to 46 metric tons ha^{-1} rototilled after application
4. Peat, applied to a uniform depth of 14 cm and rototilled

Planting of test plant species was accomplished immediately following amendment application in June 1977. Since then numerous soil biological parameters have been monitored on a regular basis in each amendment regime. These parameters include fungal community structure and standing crop, actinomycete and bacterial numbers, total microbial biomass, decomposition rates of standard substrates, N_2 fixation (symbiotic) and rates of mycorrhizal development (ecto- and VA).

In the present contribution data on fungal development in tailing sand as affected by surface amendation will be presented, this will include basic data on mycorrhizal development in two of the test plant species (i.e. jack pine and slender wheat).

GENERAL SOIL FUNGI

Qualitative studies on the fungi present in the tailing sand following each type of amendment were made two weeks after amendment applications in 1977 (i.e. prior to any plant growth) and 15 months following these applications i.e. in 1978 after two plant growing seasons. At each sampling time replicate soil samples were taken from the 0-5 cm depth of each type of amended sand; however, at the second sampling time soil samples were taken only from plots on which slender wheat was growing.

Isolation of fungi was accomplished using a soil washing method (Bissett and Widden, 1972). Washed soil particles were plated onto 2% malt extract agar containing aureomycin and streptomycin. The plates were incubated at 15°C, and fungal colonies developing on the isolation plates were sub-cultured and held for identification.

TABLE 2. Summary of fungi most frequently isolated from each type of amended tailing sand (0-5 cm depth) in June 1977 and September 1978. (Figures represent % frequency of occurrence)

Fungi isolated	Control		Fertilizer		Sewage		Peat	
	1977	1978	1977	1978	1977	1978	1977	1978
Acremonium strictum	0	0.8	0	0	0	25.0	0	0
Aureobasidium bolleyi	0	6.7	0	4.2	0	25.0	0	15.0
Chrysosporium pannorum	0	0.8	0	0.8	0	3.3	15.0	5.0
Chrysosporium verrucosum	0	0.8	0	0.8	0	3.3	5.8	8.3
Cladosporium cladosporioides	0	1.7	0	6.7	0	21.7	2.5	4.2
Cladosporium herbarum	5.8	3.3	0	1.7	0.8	0.8	2.5	3.3
Fusarium spp.	0	0	0	1.7	0.8	16.7	2.5	5.8
Mortierella spp.	0	1.7	0	0	0	4.2	7.5	5.0
Mucor hiemalis	0	0	0	0	0	36.7	0	0.8
Oidiodendron echinulatum	0	0	0	0	0	0	10.0	0.8
Penicillium spp.	0.8	1.7	0	0	0.8	0	11.7	4.2
Phialophora spp.	0	0.8	0	10.8	0	0	10.0	2.5
Phoma spp.	0	0	0	1.7	0	18.3	4.2	4.2
Trichoderma hamatum	0	0	0	0	0	0	11.7	5.8
Trichoderma harzianum	0	0	0	0	0	0	5.0	3.3
Trichoderma polysporum	0	0	0	0	0	0	14.2	7.5
Trichoderma viride	0	0	0	0	0	0.8	6.7	0.8
Sterile dark forms	1.7	13.3	0.8	15.0	0	1.7	5.0	5.8
Yeasts	6.7	18.3	4.2	25.0	0.8	27.5	0.8	5.8

Table 2 summarizes the isolation data obtained at the two sampling times. From these data it can be seen that in 1977, shortly after amendment application, a small number of fungal taxa of low frequency of occurrence were isolated from all types of amended sand with the exception of the peat amendment.

Given the rates of amendment application, it is obvious that fungi present in the amendments would form a potentially major 'inoculum' source to the tailing sand. With respect to the peat used as an amendment, the most frequently encountered fungi were *Chrysosporium* spp., *Mortierella* spp., *Penicillium* spp., Sterile hyaline forms, *Trichoderma* spp. and Yeasts. It can be seen (Table 2) that these fungi, with the exception of Sterile hyaline forms and Yeasts, formed the majority of the fungal isolates from peat amended sand at the two week sampling time.

Such a phenomenon was not seen in the sewage amended plots. The sewage sludge, prior to application, contained a significant fungal community with the most frequently isolated taxa being *Chrysosporium* spp., *Penicillium* spp., Sterile hyaline forms, and Yeasts. However the isolation data from sewage amended sand at the two week phase yielded very few isolates. This could be a result of the method of application of the amendment, in which the sewage sludge (initially containing c. 85% moisture) was spread, allowed to dry on the surface of the sand, and then rototilled into the upper layer of the sand.

Comparison of isolation data obtained in 1977 and 1978 indicates that the diversity of fungi isolated after two growing seasons (i.e. in 1978) had increased in the control sand and in the fertilizer and sewage amended sand. The sewage amendment had the greatest effects in increasing the diversity of fungal taxa. Presumably these effects were direct (because of the input of organic and inorganic nutrients in the sewage) and indirect (because of the stimulatory influence of sewage on test plant growth, and the subsequent enhanced input of nutrients by the plants).

In the peat amended sand the number of species isolated had not changed in 1978 as compared with the 1977 data. The most frequently isolated taxa also remained much the same (although in most cases appearing with somewhat decreased frequency), however *Aureobasidium bolleyi* was isolated regularly for the first time in 1978.

Data on fungi introduced to the sand via the amendments have been mentioned earlier, however other inoculum input could come from both the air spora and from the seed (or other plant material) planted in the sand. In the case of the present study air spora analysis indicated that *Cladosporium cladosporioides*, *C. herbarum*, *Epicoccum purpurescens* and white Yeasts were the major species present. Studies of fungi present on the seed coat of slender wheat showed *Penicillium* spp., *Epicoccum purpurescens*, *Trichothecium roseum*, *Alternaria alternata*, and the *Arthrinium* state of *Apiospora montagnei* to be the most frequently isolated species. Considering these data in the light of data given in Table 2 it must be concluded that fungi introduced into the sand via the planted seed played little, if any, part in recolonization of the variously amended tailing sand.

Quantitative data on amounts of fungal hyphae in each type of amended tailing sand were obtained from replicate samples of each type of amended tailing sand using a modified Jones and Mollison (1948) method. Also, total microbial biomass assessments were made using the Anderson and Domsch (1978) method. Data obtained for samples taken in 1977 by the use of these methods are given in Table 3.

TABLE 3. Fungal hyphal lengths and total microbial biomass in 0-5 cm samples of each type of amended tailing sand taken in 1977.

Type of amendment	Total hyphal length ($m\ g\ dwt^{-1}$)	Length of hyphae with cell contents ($m\ g\ dwt^{-1}$)	Total microbial biomass ($mg\ C.100\ g\ dwt^{-1}$)
Control	102.2	80.9	4.0^a
Fertilizer	29.9	15.3	1.6^b
Sewage	73.4	52.5	17.3^c
Peat	1234.5	246.3	106.7^d

(Values superscripted differently differ significantly $p = 0.05$)

The direct observation data on hyphal lengths indicated a higher amount of fungal hyphae in the initial samples from the control (unamended) sand than might be expected given the poor nutrient and organic status of that substratum. Another interesting feature of these data is the high percentage of observed hyphae which contained cell contents. From both fungal and total microbial biomass data it is clear that the fertilizer amendation yielded a significant depression of microbial development in the tailing sand in the period immediately following amendation.

The quantitative data substantiate the qualitative data discussed earlier in that, in the initial period following amendation, it was only in peat amended sand that substantial fungal development occurred. In all other amendations fungi were sparse both in terms of species diversity and in terms of amounts of mycelium.

MYCORRHIZAL ASSOCIATIONS

Endomycorrhizal development was studied in the root systems of slender wheat in the first growing season (1977). Root samples were taken at ten weeks after emergence. At this sampling time three replicate samples, each of five intact plants, were taken from each of the four types of amended tailing sand. In the laboratory, the roots were thoroughly tap-water washed on a 2 mm sieve to remove adhering soil. Then the root systems were cut into 1 cm pieces and stained using the procedure described by Phillips and Hayman (1970).

Mycorrhizal infection of the roots was quantified using the line intersect method (Olson, 1950). Four types of observation were made: length per plant with arbuscules only, length per plant with arbuscules and vesicles, length per plant with hyphae only, and, length per plant uninfected. The data obtained are given in Table 4.

TABLE 4. Effect of amendation of tailing sand on endomycorrhizal development of slender wheat after one growing season.

Amendment	Root length (cm)/plant Total	Infected	Hyphae	Arbuscules	Vesicles	Percent Infection
Control	63^{a}	1	1	0	0	1
Peat	164^{ab}	37	30	5	2	23
Fertilizer	543^{c}	0	0	0	0	0
Sewage	323^{bc}	0	0	0	0	0

(For total root length, values superscripted differently, differ at $p = 0.05$)

The data show that endomycorrhizal infection was highest in peat amended sand, it was detected at only a very low level in control sand, and was absent in plants grown in fertilizer and sewage amended sand. The higher rate of endomycorrhizal infection in plants from the peat amended sand is, presumably, the result of the presence of inoculum of suitable mycorrhizal fungi in the peat applied as a surface amendment. The application of surface amendments containing substantial endomycorrhizal inoculum may be necessary for sustained (long term) plant development in locations of severe soil disturbance. Even after 2 growing seasons (detailed data not given here), endomycorrhizal infection was not detected in plants grown in sewage amended sand, whilst plants from unamended (control) sand and fertilizer amended sand did show light infection.

Factors such as soil structure, nutrient concentrations, organic matter content and soil temperature may play roles in effectively restricting mycorrhizal development in slender wheat plants grown in control, fertilizer and sewage amended sand. The possibility that components of the general root surface mycoflora may be either inhibiting development of mycorrhizal fungi, or may be competing effectively with these fungi at the root surface under certain amendment regimes, cannot be overlooked. Certainly the root surface mycoflora of slender wheat plants after 10 weeks growth in each type of amended sand showed considerable differences; these are summarized in Table 5.

TABLE 5. Most frequently isolated fungi from the root surface of slender wheat plants grown in each type of amended tailing sand.

a. Most frequently isolated taxa:

Control	Fertilizer	Sewage	Peat
Alternaria *Fusarium* Sterile brown forms	*Epicoccum* Yeasts	*Acremonium* *Cladosporium* *Fusarium* *Geotrichum*	*Chrysosporium* *Cylindrocarpon* *Trichoderma* Sterile dark forms

b. % root segments yielding no fungi:

Control	Fertilizer	Sewage	Peat
24	44	23	29

Ectomycorrhizal development was studied in jack pine root systems in the 1977 and 1978 growing seasons. Container grown jack pine seedlings were planted in each type of amended sand, and at the end of each growing season replicate intact plants were sampled and the roots which had grown out from the original planting 'plug' were examined under the dissecting microscope and each short root was rated as infected or not. Frequent, detailed, microscopic examinations using squash preparations or sections were necessary to make accurate ratings. Data on % mycorrhizal infection are given in Table 6.

TABLE 6. Effect of amendation of tailing sand on ectomycorrhizal development in jack pine. (Figures indicate % short roots showing mycorrhizae)

Amendment	1977	1978
Control	6.9	33.5^{a}
Fertilizer	4.6	24.5^{a}
Sewage	4.6	49.4^{ab}
Peat	25.0	72.2^{b}

Values superscripted differently are significantly different ($p = 0.05$).

The 1977 data indicate that, with the exception of plants grown in peat amended sand, the presence of mycorrhizae was low at the end of the first growing season. It would appear that the tailing sand contained very small, if any, mycorrhizal inoculum. Furthermore, it appears that mycorrhizal fungi which had developed in the containerized root 'plug' during greenhouse growth prior to planting out in the sand were unable to infect roots which grew out from the 'plug'.

In the plant samples taken at the end of the 1978 growing season the highest level of ectomycorrhizal infection had, once again, occurred in the peat amended sand. However, substantial increases in infection had occurred in the other 3 types of amended sand. In the case of ectomycorrhizal infection of jack pine sewage did not appear to have any inhibitory effects. Certainly different amendments appeared to affect root growth and morphology. Thus, sewage amendment decreased the initiation of short roots, whilst, in the control sand, root weight per unit root length was less than in other amendments (presumably reflecting the low nutrient levels in unamended sand).

Whilst the sewage amendment did not appear to inhibit ectomycorrhizal development in jack pine, it is possible that other subtle effects may attend the use of this amendment. Direct isolations of symbionts from mycorrhizal roots of jack pine were made (both from inside and outside the planting 'plug'). *Thelephora terrestris* was the dominant isolate from plants in the control, fertilizer and sewage amended sand, but was isolated with only 5% frequency from plants grown in peat amended sand. *Suillus tomentosus* was also isolated in substantial amounts from plants grown in all types of amended sand except the sewage amendment where it was completely absent (both on roots inside and outside the planting 'plug'). Once again it is difficult, at this time, to explain this in terms of either abiotic or biotic factors.

The foregoing data on general soil fungi and on mycorrhizal fungi indicate the differing and complex effects of each of the chosen surface amendments on the development of fungi in tailing sand. Of these amendments, sewage is probably the most interesting in that it allowed (over the 15 month period described here) the development of a diverse mycoflora yet had apparently complex effects on the development of mycorrhizal fungi. Other data, not presented here, have indicated that another effect of sewage amendment was to reduce symbiotic N_2 fixation in sainfoin (as compared with the effects of other amendments). On the other hand, rates of cellulose decomposition in sewage amended plots were, comparatively, very high (89% dry weight loss in 12 months as compared with 0.6% in unamended sand, 13% in peat amended sand, and 32% in fertilizer amended sand).

In practical terms, final evaluation of the efficiency of surface amendments in the reclamation of disturbed land will rest on their effects in accelerating the establishment of a stabilized ecosystem. While development of primary producers is the most apparent criterion for assessing such ecosystem establishment, it must not be forgotten that direct and indirect interactions between primary producers and decomposers do indeed play a major role in this process.

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FUNGAL SPECIES ISOLATED FROM THE SENESCENT LEAVES OF *Neyraudia arundinacea* GROWING ON AREAS DISTURBED BY IRON-ORE MINING ACTIVITIES

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ABSTRACT

The present investigation is an attempt to study the fungal population isolated from the senescent leaves of Neyraudia arundinacea growing on the areas disturbed by the activities of iron-ore mining as fungi play an important role in the recycling process in this man-made habitat.

Four locations were chosen for the study: the old iron-ore dumps, the new dumps, the iron-ore tailings and an unaffected site. Senescent leaves of N. arundinacea and the associated soil samples were collected from the four sites for analysising the contents of different metals (Ca, Mg, K, Na, Fe, Mn, Zn, Cu and Pb). Fungi were also isolated from the leaves using malt agar extract agar and Czapek Dox agar.

The soil and vegetation collected from the disturbed areas contained a higher level of metals when compared with the unaffected site. N. arundinacea growing on the affected areas had a smaller number of fungal species and total number of colonies with exception of those growing on the old iron-ore dumps. They also supported a different group of fungal flora when compared with those isolated from the plants growing on the control site.

INTRODUCTION

The effects of the iron-ore tailings deposited at the east coast of Tolo Harbour, an almost landlocked sea, have been reported. The area is almost devoid of vegetation. The soil and the surrounding seawater contain a rather high level of various heavy metals, e.g. Fe, Mn, Zn, Pb and Cu (Wong et al., 1978a). Vegetation growing on the tailings was found to contain a rather high level of these metals (Wong and Tam, 1977; Kwan, 1979). Higher concentrations of these metals were also revealed in other organisms inhabiting the tailings, e.g. Paphia so. (clam) (Wong and Li, 1977) and Scopimera intermedia (crab) (Wong et al., 1978b).

There is an urgency to improve the delicate environment of Tolo Harbour which is shallow and has only a narrow outlet. The harbour has been constantly reduced in size due to the construction of Plover Cove Reservoir by linking several islands, pumping out the seawater and replacing it with freshwater as well as the recent reclamation of Shatin New Town.

An ultimate solution for improving the tailings deposited on the east coast of Tolo Harbour is to reclaim the area using grass species which are able to adapt to such a hazardous environment. A large amount of rainwater would return to the atmosphere by evapor-transpiration and the volumn of effluent water would be reduced and hence the escape of pollutants to the sea, and the effects on marine organisms would be mitigated.

Soil fungi have an important part in the building up and maintenance of soil fertility. An early report has shown a phenomena of fungal succession according to the different ages of the tailing deposits (Wong et al., 1978b). The appearance of these common soil fungi in the tailings indicates that the area is inhabitable and can be converted into a more fertile area.

A series of experiments has been commenced for improving the contaminated area with the dual purposes of minimizing the pollution problem of the surrounding areas as well as altering the unsightly waste heaps.

This paper reported the fungal species isolated from the senescent leaves of N. arundinacea, one of the most dominant plant species growing on the areas contaminated by the activities of iron-ore mining. The metal contents of the vegetation and the corresponding soil were also analysed. A subsequent paper will report on the decomposition rate of the leaves and the release of various ions during decomposition over a period of tweleve months.

DESCRIPTIONS OF THE STUDY SITES

The detailed descriptions of the surroundings of the iron-ore mine have been reported (Wong and Tam, 1977; Wong et al., 1978a; Kwan, 1979). Four sampling sites were chosen for the present study.

Site 1 (Tailings) was located at the east coast of Tolo Harbour, 2.6 km to the north west of the mine. It consisted of a sparse vegetation cover (mainly N. arundinacea) with the average bare ground of a bout 85%.

Site 2 (New waste rock dumps) was the largest terrace of the southern waste rock dumps of the mine. N. arundinacea and other taller grasses were abundant in this area with an average bare ground of 45%.

Site 3 (Old waste rock dumps) consisted of several small waste rock dumps deposited from open-cast mining 5.5 km north west of the mine. They were composed of mainly gravel ranging from 0.5-20 cm in diameter. N. arundinacea and some short grass species were found growing abundantly with significant litter accumulation. Desmodium sp. also had a high coverage.

Site 4 (Control area) was an uncontaminated area, 5 km away from the main road leading to the mine site from the shore. It consisted of a moderate plant cover (mainly N. arundinacea) as well as decomposing plant litter.

MATERIALS AND METHODS

1. Soil analysis

The surface soil samples of the four sampling sites were collected. After being air-dried at $25 \pm 2^\circ C$, they were passed through a 2 mm mesh sieve before the following analyses were conducted:

Air-dried moisture (the weight difference before and after the soil samples were dried at $105^\circ C$ for four hours); texture (Bouyoucos, 1951); pH (soil: water, 1:2.5 using a pH meter); organic carbon (Walkley and Black, 1934); water-soluble phosphorus (Watanabe and Olsen, 1962); total nitrogen (semi-micro Kjeldahl method; Bremner, 1960); total cation exchange capacity (Hesse, 1971); individual exchangeable cations (atomic absorption spectrophotometry after the samples had been extracted by 1M ammonium acetate) and the total metal contents (atomic absorption spectrophotometry after the samples had been digested by mixed acid, $HNO_3:HClO_4:H_2SO_4=10:4:1$; Allen et al., 1974).

2. Metal contents of senescent leaves of N. arundinacea

Senescent leaves of N. arundinacea were collected from the four sampling sites. The amount of various metals were analysed by means of atomic absorption spectrophotometry after the samples had been digested by mixed acid, $HNO_3:HClO_4:H_2SO_4=5:0.5:1$; Allen et al., 1974).

3. Fungal species isolated from the senescent leaves

The fungal flora was isolated from the senescent leaves of N. arundinacea using malt extract agar and Czapek Dox agar after the litter had been washed with 1% Teepol (7 changes) and then distilled water (8 changes). The number of colonies was estimated and the fungal species identified.

RESULTS AND DISCUSSION

1. Soil analysis

The results of soil analysis are shown in Tables 1 and 2. Soil samples from Site 1 (Tailings) were alkaline (pH 8.22), sandy (92.8%), lacked total organic carbon (0.07%) and total nitrogen (0.14%); but contained comparatively high contents of water-soluble phosphorus (0.84 ppm), total cation exchange capacity (13.68 m.e./100 g soil) as well as total and exchangeable individual metal ions particularly Mn, Fe, Zn, Pb and Cu.

TABLE 1 The edaphic properties of the sampling sites (Each value is a mean of three samples).

	1 Tailings	2 New dumps	3 Old dumps	4 Control
Air-dried moisture %	1.3	3.8	3.0	4.7
pH	8.22	6.89	4.82	4.46
Texture: sand %	92.8	58.8	67.8	52.8
silt %	1.4	21.2	19.2	20.0
clay %	5.8	20.0	13.0	27.2
Total organic carbon %	0.07	0.28	0.18	0.96
Total nitrogen %	0.14	0.33	0.24	0.43
Water-soluble phosphorus ppm	0.84	0.64	0.83	0.33
Total cation exchange capacity m.e./100 g	13.68	12.94	12.98	9.56

Site 2 (New waste rock dumps) and Site 3 (Old waste rock dumps) had comparable edaphic properties. However, Site 2 had a higher pH value (6.89 compared with 4.82 at Site 3), less sandy (59% compared with 68% at Site 3), and contained higher levels of total organic carbon (0.28% compared with 0.18%), and total nitrogen (0.33% compared with 0.24%). However, the content of water-soluble phosphorus was lower (0.64 ppm compared with 0.83 ppm). The contents of total cation exchange capacity were similar at both sites (12.9 m.e./100 g soil). These two sites also had comparable metal contents, both in terms of total and exchangeable contents although Site 2 contained higher levels of most metals except Mn and Cu.

TABLE 2 The metal contents of soil samples collected from different sites (Each value is a mean of five samples: mean±standard error. a=exchangeable content, b=total content).

ppm		Site 1 Tailings	Site 2 New dumps	Site 3 Old dumps	Site 4 Control
Na	a	190.1 ± 3.9	12.5 ± 0.1	2.8 ± 0.3	8.1 ± 0.4
	b	598.6 ± 64.5	708.4 ± 71.7	342.3 ± 11.7	208.4 ± 28.2
K	a	57.1 ± 1.0	54.7 ± 9.4	24.5 ± 0.8	35.4 ± 0.5
	b	2018.2 ± 42.7	5514.3 ± 216.6	8586.0 ±247.2	1678.6 ± 198.8
Ca	a	433.3 ± 4.0	116.0 ± 45.3	10.0 ± 1.2	36.5 ± 1.9
	b	2405.4 ±258.3	727.7 ± 181.6	25.7 ± 1.4	42.2 ± 5.2
Mg	a	150.0 ± 2.4	220.0 ± 67.1	37.6 ± 0.8	58.7 ± 0.7
	b	7116.2 ±371.4	3381.3 ± 158.2	1741.7 ± 95.0	74.7 ± 6.2
Mn	a	25.64 ± 0.9	4.75 ± 0.9	7.20 ± 0.4	3.40 ± 0.4
	b	2123.8 ± 51.8	1216.4 ± 231.8	1412.7 ±132.8	191.9 ± 22.9
Fe	a	6.67 ± 0.3	3.50 ± 0.4	1.40 ± 0.3	0.40 ± 0.2
	b	12908.8 ±1284.9	8180.3 ±1584.6	17469.9 ±1753.3	5278.8 ± 426.3
Zn	a	10.10 ± 0.2	2.00 ± 0.4	1.30 ± 0.1	0.60 ± 0.0
	b	261.4 ± 15.3	227.7 ± 12.1	200.4 ± 17.2	18.2 ± 2.9
Pb	a	0.73 ± 0.6	8.20 ± 2.0	3.80 ± 0.7	1.90 ± 0.4
	b	116.5 ± 2.6	93.9 ± 10.5	103.9 ± 27.2	73.6 ± 4.5
Cu	a	3.33	1.05	1.05	0
	b	12.6 ± 0.3	48.3 ± 2.9	115.0 ± 10.4	1.81 ± 0.9

Site 4 (Control site) was acidic with a pH of 4.46 which is common on the surface of red-yellow podzolic soils (Fitzapatrick, 1974) as well as for the soil in Hong Kong. It also contained a higher portion of fine particles (sand:53%), high contents of total organic carbon (0.96%), total nitrogen (0.43%), but lower levels of cation exchange capacity (9.6 m.e./100 g soil) and total as well as exchangeable individual metal contents, as expected.

Due to the magnesium limestone deposit of the iron ore (Davis, 1964), the contaminated areas were more alkaline and contained higher levels of various metals dervied from the waste materials. The higher content of water-soluble phosphorus originated from the parent materials of the iron-ore (Lai, 1959). The areas were usually devoid of vegetation, lacked soil profiles and contained only little soil substrates. The present iron-ore tailings had similar characteristics as the 70 to 130-year-old weathered iron-ore spoil of West Virginia (Tryon and Markus, 1953; Smith et al., 1971).

2. Metal contents of senescent leaves of N. arundinacea.

The metal contents of senescent leaves of N. arundinacea used for the isolation of fungi are listed in Table 3. However, it must be noted that the root portions of the plants contained the highest contents of all heavy metals (Fe, Zn, Pb and Cu) except Mn whereas the leaf portions contained the highest levels of macro-elements (Ca, Mg, Na and K) (Kwan, 1979). It had been shown that plants growing on waste materials contaminated with high levels of heavy metals tended to concentrate these metals in the root portions especially the cell wall fraction (Bradshaw et al., 1965; Turner, 1970). On the contrary, the high level of various macro-elements on the leaf portions might be favourable for carrying out photosynthesis.

TABLE 3 The metal contents of the senescent leaves of N. arundinacea. (Each value is a mean of 5 samples: mean±standard error).

ppm	1 Tailings	2 New dumps	3 Old dumps	4 Control
Na	1161.9±327.2	154.3± 56.2	127.0± 20.1	114.6± 32.1
K	1294.1±183.3	961.0± 80.9	493.9± 59.9	3471.2±641.2
Ca	3234.0±693.0	5285.9±1211.3	2748.8±497.0	5264.0±347.0
Mg	2880.4±366.4	1781.4± 312.2	1178.2±411.8	855.9± 36.3
Mn	185.7± 31.5	201.7± 22.3	90.5± 14.4	76.8± 11.4
Fe	869.6±209.6	531.3± 105.3	87.6± 11.8	120.2± 31.3
Zn	31.2± 33.4	18.8± 9.8	12.9± 9.1	33.9± 21.8
Pb	12.9± 11.3	9.3± 10.3	15.7± 17.7	10.7± 15.8
Cu	37.1± 36.9	24.0± 20.8	40.5± 35.4	16.2± 12.2

However, the leaf portions also contained a rather high level of various heavy metals especially Mn (Kwan, 1979). It would be interesting to know if the contents of heavy metals had any effect on the fungal flora growing on the senescent leaves of N. arundinacea, one of the most dominant higher plants growing on the contaminated sites.

According to Table 3, the leaves of N. arundinacea collected from Site 1 (Tailings) had the highest contents of Na, Mg, Fe whereas those from Site 2 (New dumps) the highest Mn and Site 3 (Old dumps) the highest Cu. Those collected from the control site (Site 4) had the highest contents of K and Ca and comparatively low levels of all other metals. In general, the metal contents in the leaves reflected the metal contents in the soil.

3. Fungal specis isolated from the senescent leaves.

The fungal species together with the number of colonies isolated from the senescent leaves of N. arundinacea are listed in Table 4. In general, the leaves collected from the contaminated areas had a smaller number of fungal species and total number of colonies with the exception of Old dumps (Site 3). Furthermore. the results also revealed that the fungal species isolated from the leaves collected from the contaminated areas were different from those collected from the control site. There were thireteen fungal species (including 1 sterile species) isolated from the contaminated areas which could not be found in the control site. There were only six fungal species (including 3 sterile species) isolated from the control site which could not be found in the contaminated areas.

When comparing the three contaminated sites, the senescent leaves of N. arundinacea collected from the tailings consisted of the smallest number of fungal species as well as the total number of colonies. Fusarium sp. was the most dominant fungal flora. The results also indicated that both Site 2 and Site 3 had similar fungal species, although the Old dumps (Site 3) had a higher total number of colonies. Both sites were dominated by Fusarium sp. but other fungal flora e.g. Phoma macrostoma, Pestaloptiopsis sp., etc. also appeared frequently. The higher number of fungal species and total number of colonies of Site 3 might be due to the lower levels of various metals especially Mn and Fe in the leaves of N. arundincea.

It has been reported that high concentrations of heavy metals in plant litter would inhibit the C and N mineralization, cellulose and starch decomposition and enzyme activity of decomposers (Tyler, 1974; 1975; 1976; Liang and Tabatabai, 1977; 1978) and results in smaller number of microorganisms (Jordon and Lechevalier, 1965; Williams et al., 1977). However, most of these studies were concerned with smelter and mine wastes which contained a very high level of heavy metals, e.g. the inhibitory effects of Pb and Zn in the mine waste and its vegetation was demonstrated by a greater accumulation of litter and less soil humus (Williams et al., 1977). The metal

TABLE 4 The fungal species isolated from the senescent leaves of *N*. *arundiacea*.

Fungal species	Site 1 Tailings	Site 2 New Dumps	Site 3 Old Dumps	Site 4 Control
Fusarium fusarioides (Frag.& Cif.)Booth	118	10	5	32
F. avenaceum (Fr.) Sacc.	1			
F. graminearum Schwabe			8	
F. equiseti (Corda) Sacc.			1	
Fusarium sp.	68	183	106	93
Phoma sorghina (Sacc.) Boerema,Dorenbosch & van Kest	1	2	4	
P. glomerata (Corda) Wollenw. & Hochapf		1		
P. macrostoma Mont.		9	20	33
Pestalotiopsis versicolor (Speg.) Steyaert	1	2		17
P. palmarum (Cooke) Steyaert			1	
Pestaloptiopsis sp.		7	26	
Trichoderma sp.			1	13
Acremonium sp.				45
Alternaria sp.				19
Massariothea themedae Syd.			16	
Curvularia lunata (Wakker) Boedijn			7	
C. eragrostidis (P. Henn) J.A. Meyer		1		
Sordaria humana (Fuckel) Wint	1	6		
Nigrospora sp.				1
Ulocladium atrum (Preuss) Simmons			1	
Rhizopus stolonifer (Ehrenb. ex Fr.) Lind	1			
Sterile sp. A	1			
B				2
C				88
D				2
Total number of species	8	9	12	11
Total number of colonies	192	201	196	345

contents of the soil and vegetation contaminated with the activities of iron-ore mining in the present study were low when compared with other reports, and a comparison could not be made as no study on the isolation of fungal flora from vegetation growing on iron-ore wastes could be traced.

The higher number of fungal species and the total number of colonies isolated from the leaves collected from the Old dumps (Site 3) might be due to the stimulation of fungal growth of the slightly higher metal contents as similar phenomena has been observed on the stimulation of root growth under a slight increase of heavy metals (McNeilly and Bradshaw, 1968).

There is also evidence that microbial populations of areas contaminated by heavy metals develop an increased tolerance to these metals (Hilton, 1967; Griffths et al., 1974; Williams et al., 1977). However, no conclusion could be drawn as to whether the fungal flora isolated from the leaves from Site 1 (Tailings) which contained a rather high level of various heavy metals were tolerant populations. Further studies should be concentrated on the toxicity of heavy metals on the fungi isolated from this area.

The leaves used for the isolation of fungal flora had been washed thoroughly so as to prevent the aerial deposition of metals on the leaf surface which would subsequently affect the fungal species isolated from the leaves. The lower number of fungal species and total number of colonies obtained from the leaves collected from the two more contaminated areas: Site 1 (Tailings) and Site 2 (New dumps) reflected that active growth of fungal hyphae penetrating the leaves contaminated with a rather high content of heavy metals was partially inhibited.

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RESPONSE OF FIELD POPULATIONS OF TARDIGRADA TO VARIOUS LEVELS OF CHRONIC LOW-LEVEL SULPHUR DIOXIDE EXPOSURE

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ABSTRACT

The soil populations of Tardigrada of a northern mixed-grass prairie were sampled after having been exposed to various chronic low levels of sulfur dioxide. The populations of two different sites showed substantial reduction, although it was difficult to show the reductions were significant, due to high variability of sample counts. Substantial reduction in the frequency of occurrence in the samples helped to substantiate the population decreases. Three genera of tardigrada have been identified from sample material: Macrobiotus Shultze, Hexapodibius, and Diphascon Plate.

INTRODUCTION

Along with the ever-increasing energy demands of the world, there is an accompanying demand for utilization of fossil fuels other than petroleum. Foremost among the non-petroleum fossil fuels is coal. The in-place use of large coal deposits in the North American midwest for electrical power production is rapidly expanding and along with this development is the accompanying problem of our pollutants and the effects on the vast grassland ranges under which the coal deposits occur. The impact of coal-fired power plant emissions on native grasslands is currently the central subject of the U.S. Environmental Protection Agency - supported Montana Coal Fired Power Plant Project (CFPP) (Lewis et al. 1976). Attempts have been and are continuing to be made on evaluating the effects of air pollutants, especially SO_2, on many of the component parts of the grassland system in southeastern Montana.

Although the biological effects of air pollutants, particularly SO_2, have received extensive attention, especially for plants, comparatively little attention has been directed to other segments of either natural or agroecosystems. Detailed studies on the effect of SO_2 on the soil and its flora and fauna are almost nonexistant. As part of the CFPP study, soil nematode populations were being censused after having been exposed to various levels of chronic low-level SO_2 concentrations (detailed discussion will follow). From the same samples it was noticed that tardigrade populations appeared to be declining with increased SO_2 concentrations. These findings precipitated this study.

Tardigrades are small (<1.0 mm) arthropod-like animals generally referred to as "water bears" because most known species are aquatic or semiaquatic in habit. Very little is known about these animacules even to the point that there is disagreement among the few scientists working with them as to where they belong phylogenetically (Riggin, 1962). Some people have given them separate phylum status while others have included them in the arthropods. The functional or trophic status of tardigrades is unknown, however, a few studies have shown that fairly substantial populations do occur in certain soil systems (Franz, 1941, 1950; Ramazzotti, 1959). Population estimates range as high as $300{,}000 \cdot m^{-2}$. Generally, the Tardigrades are overlooked in soil faunal studies since most commonly used extraction methods are inefficient in retrieving them. Even though they may have a relatively minor role in soil ecosystem function when compared to such things as nematodes, their importance in this study lies in the fact that they may be very sensitive indicators of what the effects of air pollutants are on the soil ecosystem processes.

METHODS AND MATERIALS

Study area

The study area was located in southeastern Montana within the Custer National Forest. The habitat type is classified as northern mixed grass prairie with western wheatgrass (Agropyron smithii Rydb.) the dominant grass species. Two study sites were located on rolling uplands with southwest slopes of less than 4°. Soils of both sites were derived from outwash of parent material from nearby buttes and ridges. Site I had a well developed grassland soil with a silty loam texture, moderate permeability and water retention capacity; while Site II had a silty clay loam soil with lower permeability and higher water retention capacity.

The climate of the area is continental, semiarid, and extremely variable. Approximately half of the average annual precipitation of 360 mm is received in April, May, and June. The average annual temperature is 7°C with an average 130-day frost-free growing season. Grasses and forbs associated with the dominant western wheatgrass include prairie Junegrass [Koeleria cristata (L.) Pers.], Sandberg bluegrass (Poa secunda Presl.), needle-and-thread grass (Stipa comata Trin & Rupr.), western yarrow (Achillea millefolium L.), common dandelion (Taraxacum officinale Weber), and goatsbeard (Tragopogon dubius Scop.).

Methods

Four plots (0.52 ha each) at Site I were exposed to controlled levels of sulfur dioxide during the growing season for four years (1975-1978) with four similar plots at Site II exposed for three years

(1976-1978). Sulfur dioxide was distributed over the plots through a network of perforated aluminum pipes located approximately 0.75 m above the soil surface (Lee and Lewis 1978). Concentrations within the canopy of each plot were measured hourly with a Meloy Laboratory sulfur analyzer (Model SA 160-2). Sulfur dioxide was applied to the plots at a constant rate and logrithmic variations in SO_2 concentrations resulted from variations in meteorological conditions, primarily wind speed. Monthly median sulfur dioxide concentrations were zero for the control, 52 $\mu g \cdot m^{-3}$ for the low, 105 $\mu g \cdot m^{-3}$ for the medium, and 183 $\mu g \cdot m^{-3}$ for the high concentration treatment. Each treatment plot was divided into two equal replicates.

Each site was sampled once at midseason (July) in 1977 and 1978. Site I was sampled again in late 1978 (September). Samples consisted of soil cores 5.0 cm diameter by 10.0 cm deep taken randomly within the treated plots. Sampling points were determined by a random numbers table. Sample size was five per replicate (10 per treatment) except in September 1978 when the sample size was doubled to 10 per replicate. The tardigrades were extracted by a Baermann funnel process which is a commonly used live or dynamic extraction technique. Specimens were preserved in 70% ethynol and representatives were sent out for identification.

RESULTS

Three genera of tardigrades have been identified to date from the material collected, although none have been identified to species. The identified genera include Macrobiotus Schultze, Hexapodibius, and Diphascon Plate (=Hypsibius Ehrenberg). The Diphascon is probably undescribed and further work with the other two genera is needed to determine if they fit recognized species.

The mean counts for all sample dates show substantially reduced populations in the high treatment plots and variously reduced populations in the intermediate treatments (Figures 1 and 2). As with most field census data, high variability seriously hampered interpretation of the results. A repeated measures analysis of variance was used to test for significant treatment effects. The ANOVA was run on both the raw and transformed data, the transformation being a log transformation by the formula:

$$\text{Log } (X+1)$$

The transformation was used because the variance tended to be larger with the larger means plus the occurrence of a large number of zero counts in the higher treatment plots.

The ANOVA results tend not to show as significant a treatment effect as might be expected from initial evaluation of the data. For Site I (July dates in 1977 and 1978), a significant treatment effect was found in the raw data ($P = .0545$) but not in the transformed data ($P \overline{<} .10$). No significant treatment effect was found in either the

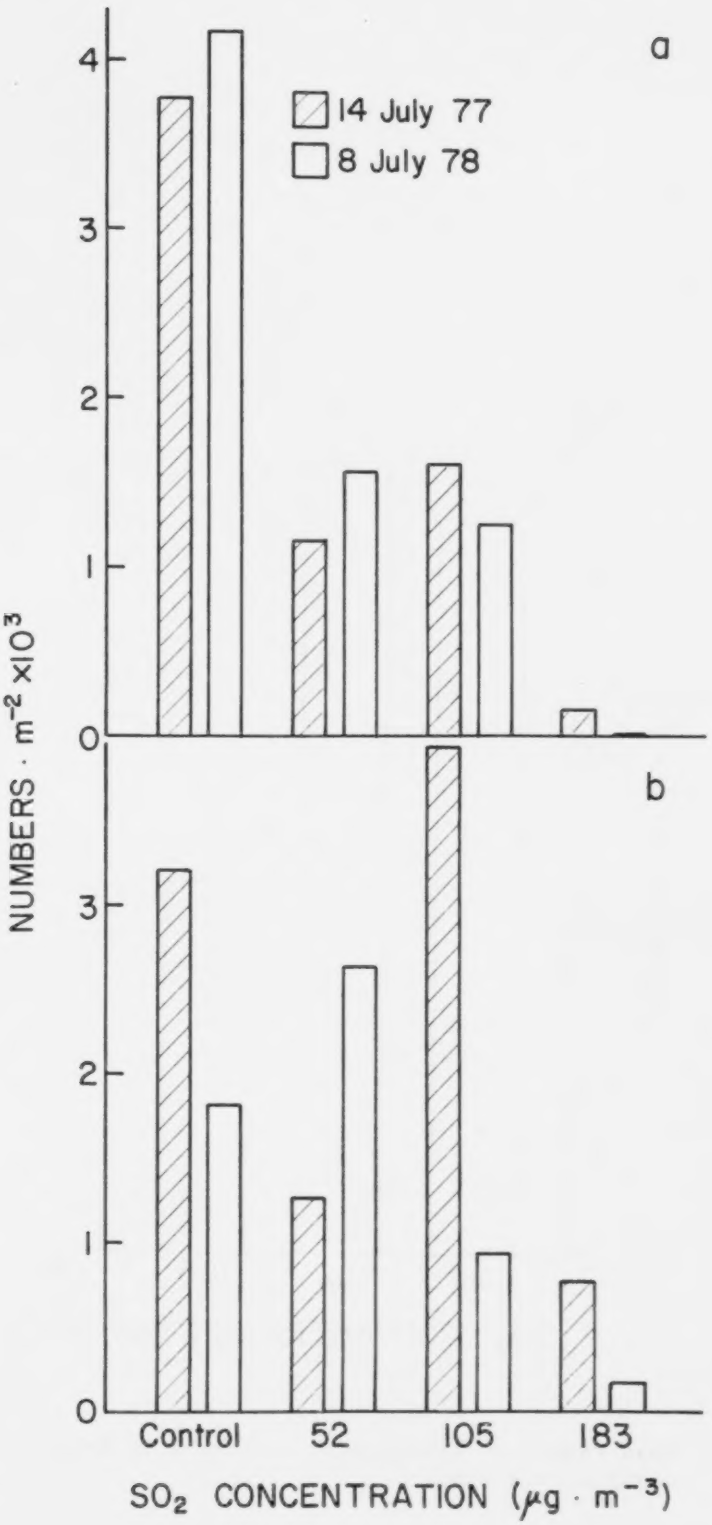

FIGURE 1. Mean counts of Tardigrades on two field sites in southeastern Montana in 1977 and 1978 (a = Site I and b = Site II).

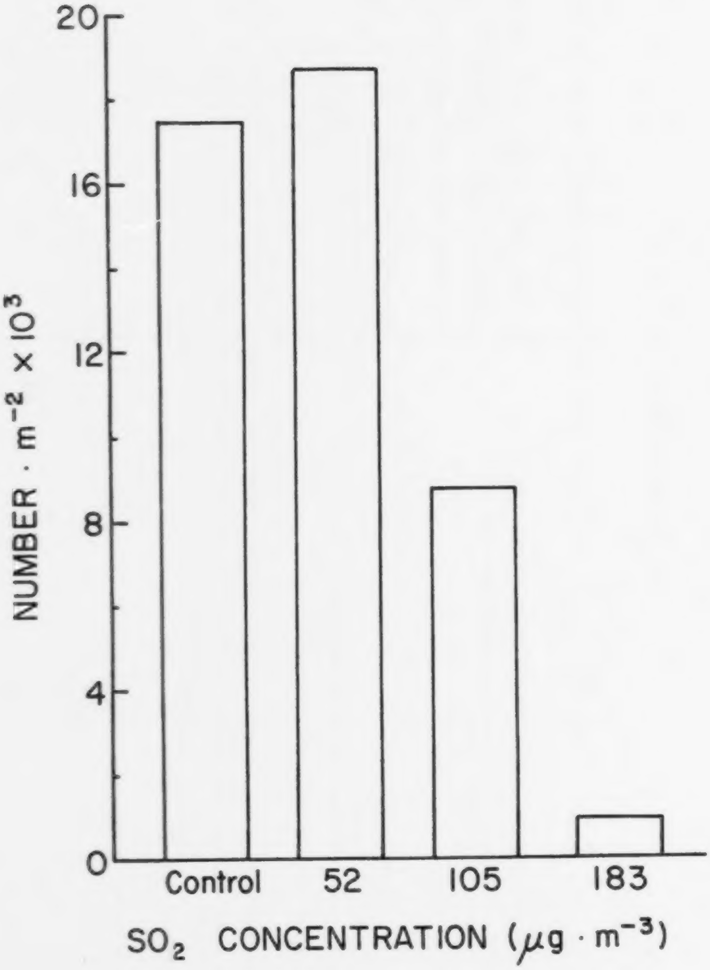

FIGURE 2. Mean counts of Tardigrades on Site I in September, 1978 in southeastern Montana.

raw or transformed data on Site I on September 16, 1978. The significant treatment differences in the July dates were between the control and high treatment only. For Site II, a significant treatment effect between the control and high treatment occurred for both the raw and transformed data (P = .0313 and .0898 for raw and transformed, respectively).

The frequency of occurrence of tardigrades in the samples was calculated for all sample dates (Table 1). The results show a substantial reduction in frequency with increased SO_2 concentration. The decrease was greater for Site I than for Site II, from 90% to 16.7% for Site I as compared with 60% to 15% for Site II.

TABLE 1 FREQUENCY OF OCCURRENCE OF TARDIGRADES IN SAMPLES

	Treatments			
Dates	Control	Low	Medium	High
		Site I		
14 July 77	80	70	60	20
8 July 78	100	90	30	0
16 Sept. 78	90	75	80	30
$\bar{X}$	90	78.33	56.67	16.67
		Site II		
14 July 77	60	20	30	20
8 July 78	60	30	20	10
$\bar{X}$	60	25	25	15
		Total		
$\bar{X}$	78.0	57.0	44.0	16.00
S.E.	8.00	13.56	11.22	5.10

CONCLUSIONS AND DISCUSSION

The occurrence of at least three species of tardigrades on the sites has added confusion to the interpretation of the census data because only total counts were made on each sample. The individuals were not identified to species, therefore it is not known if the reduced population sizes were the result of all species being affected or just one or two. A qualitative analysis of the sample material sent out for identification showed a majority of the specimens were Macrobiotus.

Although the substantially reduced tardigrade populations in the treated plots were not easily shown to be statistically significant, we are confident the reductions are real. The consistantly reduced frequency of occurrence in the samples helps to support this conclusion. The high variability of counts among the samples from the control and low treatment plots was undoubtedly the principal reason for lack of good statistical confirmation. The high variability of the data is not surprising since tardigrades, like nearly all organisms probably have variously clumped distributions and the sample core size (18.1 cm^2 surface area) was probably too small to reduce or eliminate the clumping problem.

At this writing, additional sampling of the treated plots is being done in a continuing effort to get more concrete evidence of the effects of SO_2. A preliminary attempt to determine the vertical distribution of the tardigrades has shown they are essentially restricted to the surface 1 to 2 cm of the soil profile. Based on this knowledge, future sampling will focus on increasing the surface area of the soil core samples while reducing the depth so as to hopefully reduce the variability of the data.

Since the tardigrade population is apparently restricted to the soil surface, they, as a whole, may be much more vulnerable to SO_2 and other air pollutants than other soil faunal groups such as nematodes and microarthropods since these occur at deeper levels of the soil profile where any effects of SO_2, etc., may be buffered out by the soil. At this writing, further studies are planned to investigate our hypothesis that for the soil SO_2 will have its major impact at or very near the surface. This impact will ultimately be manifest in reduced decomposition rates of litter material.

ACKNOWLEDGMENTS

We wish to thank those people who gave assistance at various times in this study including Ms. Marilyn Campion for statistical analysis, Richard Nielson and Robin Cox for assistance in sample processing and counting, and Mr. R. O. Schuster, University of California at Davis for identification of reference material.

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QUESTIONS and COMMENTS

D. FRECKMAN: I wonder if variability in summer numbers could be due to anhydrobiotics. Have you looked at or noticed anhydrobiotic tardigrades in the top few cm?

J.W. LEETHAM: Anhydrobiosis could possibly be responsible for some of the variability, but of greater importance would be the clumped distribution so common to most soil organisms. Anhydrobiosis could possibly be a factor in the differences between summer and fall population estimates.

B.S. AUSMUS: Why was the application made only during the growing season? It seems soil biological effects might be greatly affected by winter deposition?

J.W. LEETHAM: Part of the reason for fumigation only during the growing season is due to the mechanical difficulties encountered in trying to run the system during the severe winter. Also, the whole ecosystem functioning would be at its lowest during the winter which would result in very low exposure to functioning organisms. It is recognized that winter exposure will be an integral part of the power plant functioning and certain effects of the pollutants may result from accumulation in snow cover. However, for our study we arbitrarily chose to restrict our exposure times to the growing season only.

J. ADDISON: Since you do not fumigate your sites during the winter, I was wondering whether by·ignoring the possibility of winter deposition of SO_2 in snow you may be missing a major input of "acid rain"?

J.W. LEETHAM: (Answered along with the response to the questions by Berverly Ausmus).

M.J. MITCHELL: Do you know the actual cause of mortality?

Are you monitoring the sulfur transformations in the soil?

J. W. LEETHAM: The specific cause of mortality are unknown, but one suggestion we have put forth is that SO_2 can react with water to form sulfuric acid and this may be happening, at least periodically, at the soil surface and this possible change in soil pH may be affecting the tardigrades.

We have not, as yet, monitored the sulfur as it enters the soil, but plans are to pursue this as part of further decomposition studies.

THE EFFECT OF AN INCREASED Ra CONTENT IN THE SOIL ON SOIL ANIMALS

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The effect of background radiation on soil invertebrates under natural conditions has never been studied before.

OBJECTIVES AND METHODS

During two field seasons we studied the effect of an increased radiation level caused by a natural radionuclide radium-226 on soil animal complexes. The experimental plots with an increased level of radiation of 50-4000 μR/hr were small in area (1-2 ha). They were situated at a terrace above a river valley with a meadow vegetation in the middle taiga subzone. A higher radiation background was caused by the flooding of underground layer waters with an increased Ra content. The content of Ra in the experimental plot soil was $7.1 \cdot 10^{-10}$ to $5.6 \cdot 10^{-11}$ per gram of the annealed sample. The soils were dern-podzolic.

Control plots were similar with respect to soil and vegetation to the experimental, but had a normal natural radiation background.

Hand sifting was used to study the soil population by mesofauna at an area of 50 x 50 cm down to the level at which animals occurred (30 - 40 cm) and by microarthropods in samples 1 dm^3 in volume.

RESULTS AND DISCUSSION

The radiation levels at the plots under study varied a good deal which evidently explains a great variance of mesofauna populations from sample to sample.

Statistical treatment of material included reduction of the variants to normal distribution by the formula $x' = \lg(x+1)$, the data obtained being compared by the Student index. Highly statistically significant differences ($P < 0.01$) were obtained for all long-developing groups characterized by a relatively low motility, i.e. those which are permanent residents of plots with an increased radiation background. Such plots showed a much lower number of earthworms compared with controls, the same being true of dipteran and click-beetle larvae. Significantly lower numbers were likewise recorded in other large invertebrates (Table 1).

Table 1: POPULATION OF MEADOW RIVER VALLEY SOILS WITH SOIL MESOFAUNA IN CONTROL AND IN PLOTS WITH AN INCREASED Ra CONTENT

ANIMAL GROUP	Control		Plot with increased radiation level	
INSECTA	Total number	Mean per m^2	Total number	Mean per m^2
Diptera larvae	77	3.85	15	0.75
Elateridae larvae	77	3.85	13	0.65
Staphylinidae immatures	215	10.75	164	8.20
Carabidae immatures	29	1.45	17	0.85
Total	398	19.9	209	10.45
LUMBRICIDAE				
Eisenia nordenskioldi (Eisen.)	9	0.45	1	0.05
Dendrobaena octaedra (Sav.)	29	1.45	5	0.25
Octolasium lacteum (Oerley)	3	0.15	0	0
Others	139	6.95	56	2.80
Total	180	9.00	62	3.10

No statistically significant differences were found with respect to the numbers of actively motile surface arthropods (Staphilinidae, Carabidae, spiders and Phalangida).

The numbers of mature oribatids was 72± individuals per dm^3 in the control against 39± 8 in the radium-polluted plot, no faunistic differences being noted. No statistically significant differences were recorded as to the numbers of other groups of soil mites and springtails. Thus, soil dwellers proper, with lower motility and relatively long period of individual development can serve as a convenient bioindicators in studies of the natural radiation effect on zoocoenosis.

Earthworms proved specifically sensitive to an increase of radiation background. In fact, in mid-summer a plot with a radiation level of about $100 \mu R/hr$ contained a 7-fold reduction of earthworms over the control, the experimental earthworms also being smaller in size. Of particular interest is the fact of a reproductive disturbance. The earthworm population of the control contained a great number of young individuals, these being nearly absent in the polluted plot. Evidently at polluted plots these young individuals are retarded in growth and achievement of sex maturity compared with controls. In fact, in June when earthworms only start reproducing, their control population was represented by only sexually-mature individuals, and at experimental plots over half of the population had failed to achieve sexual-maturity by that time.

The histological structure of the epithelium of integuments and mid-gut (the tissues in direct contact with the Ra-polluted soil) in animals from control and experimental plots (with a radiation level of about $4000 \mu R/hr$) was investigated. The subject of investigation was *Dendrobaena octaedra* (Sav.) and also *Dendrodrilus rubidus* (Sav.). Both these species are dwellers of the most superficial soil layers. The material was fixed in the Bouin's solution and prepared for histological studies in a standard manner.

Dwellers of the superficial layers of soil proved to have integuments consisting of one layer of heterogenous epithelial cells and a cuticle consisting of a thin transparent membrane. The epithelial cells include narrow cylindrical ones with a small nucleus and a compact plasm and broader ones with glandular and mucousal cells filled up with a mucous secretion (Semenova 1968). This mucous secretion is excreted through cell pores, constantly moistening by the worm body which protects it from drying up. There are small cambial cells in the basal part of the epithelium.

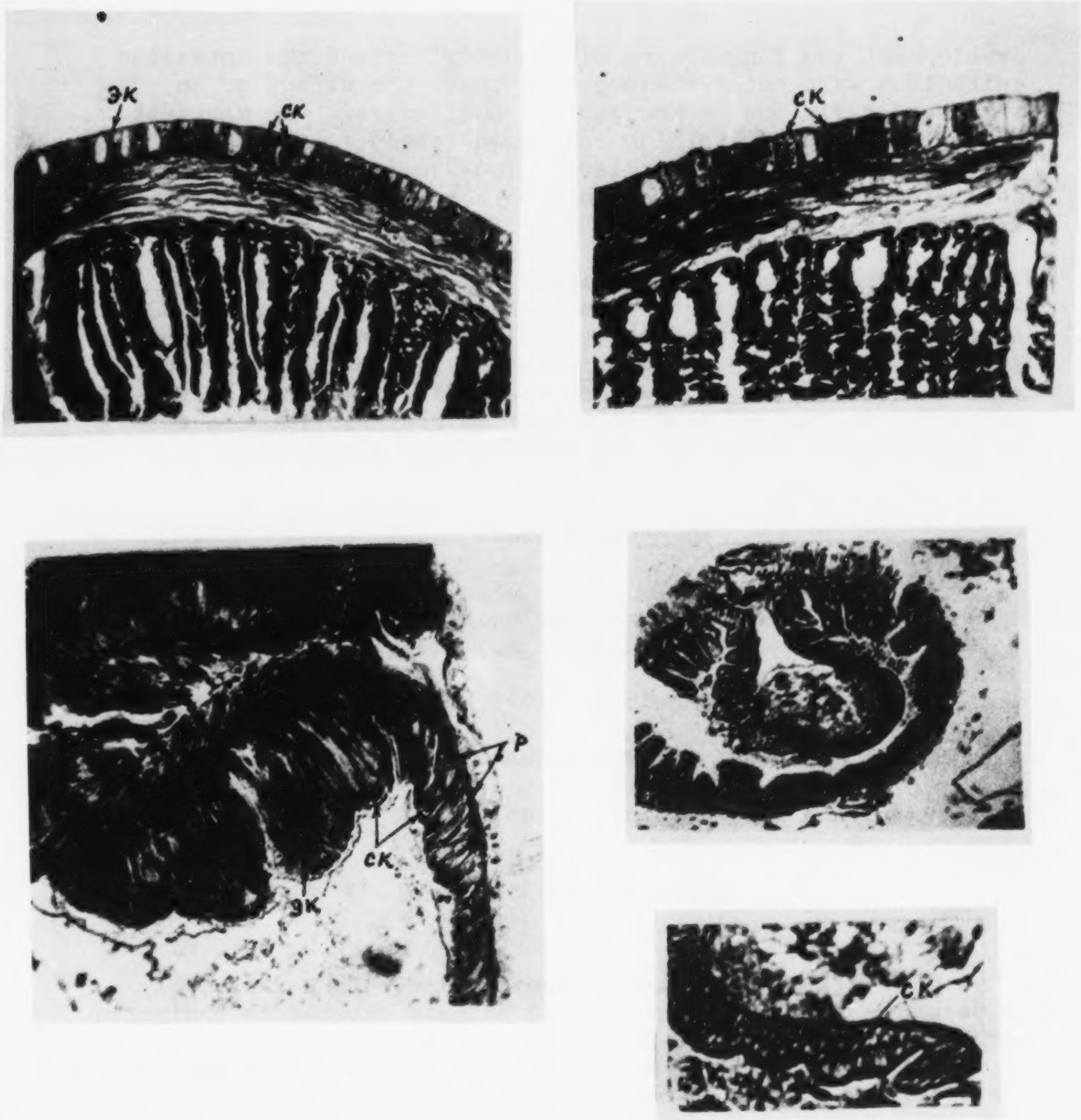
Both earthworm species under study from the control plots were characterized by a typical structure of the integuments (Figure 1,A). The earthworms collected from the Ra-polluted soil showed considerable changes in the structure of integument epithelium (shape and size of mucous cells). The mucous cells of these earthworms are broader and larger as compared with controls (Figure 1,B). The number of mucous cells in the radiation-affected earthworms is much higher than that in the control ones. There are fewer cambial cells in these sections. The structure of the mid-gut epithelium was also studied. The mid-gut epithelium was found to consist of two of the following cell types: epithelial cells which produce digestive enzymes and absorb digestion products, and mucous cells that excrete mucus to moisten the food mass. The amount of mucous and epithelial cells in the epithelial thickness is nearly similar (Semenova 1966). There are a large number of regeneration nests and individual regeneration cells in the basal part of the epithelium. The typical structure of the mid-gut described above was found in both species collected at control plots (Figure 1,B).

The earthworms collected at the experimental plot showed changes in the structure of the mid-gut epithelium: epithelial cells which produce enzymes were found in a much less number as compared with mucous cells. The number of regeneration nests and regeneration cells in the epithelial thickness is also smaller compared with that in the control earthworms (Figure 1,D).

Both species of experimental earthworms (radiation background about 100-4000μR/hr) had a considerable increase of mucous cell numbers in the epithelium of the outer integuments and mid-gut as well as an increased excretion of mucus which is evidently a protective response to the action of α-radiation.

Comparison of our data with those previcusly obtained for land vertebrates dwelling at the same plot (Maslov 1972, Maslov and Maslov 1972) showed that the general regularities are similar: the greatest radiation effect is recorded in sedative groups of long-time dwellers of plots with an increased radiation background in which disturbances in the

Figure 1.



THE STRUCTURE OF THE INTEGUMENTS OF EARTHWORMS (X 280). A-INTEGUMENTS OF *Dendrobaena octaedra* FROM CONTROL PLOTS; B - INTEGUMENTS OF *D. octaedra* FROM PLOTS WITH HIGHER RADIATION BACKGROUND; C - EPITHELIUM OF MID-GUT OF *Dendrodrilus rubidus* from CONTROL PLOTS; D - CROSS-SECTION OF MID-GUT OF *D. rubidus* FROM PLOT WITH INCREASED RADIATION BACKGROUND: ЭК. - EPITHELIAL CELLS, СК. - MUCOUS CELLS, Р - REGENERATION CELLS development and functioning of the body surface and intestine epithelium were noted. Along with that, the effect of an increased radiation background for soil animals was manifest not only at plots with high radiation levels (2000-8000 μR/hr) but also with a much lower level (100-200 μR/hr). This is evidently explained by a closer contact of soil animals with Ra-containing soil.

Earthworms are a specifically convenient subject for studies of the effect of an increased radiation background as these are not only irradiated from the outside but also from the soil they swallowed. All the rest of the land animals under study so not swallow the soil and consume only animal or vegetative food in which the radionuclide content is considerably lower (by 1-2 orders) than in the soil.

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QUESTIONS and COMMENTS

K.H. DOMSCH: The data presented indicate a relatively wide range of sensitivity of soil animals exposed to radiation. Are there also cases of increased populations?

D.A. KRIVOLUTSKY: No, we can see the decreased populations only for all groups of soil animals.

COLLEMBOLA OF REHABILITATED MINE SITES IN WESTERN AUSTRALIA

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INTRODUCTION

Bauxite mining is an important industry in Western Australia, and takes place mainly in the ranges south east of Perth where operations are currently being expanded. For the most part, areas being mined carry native Eucalyptus forest which has never been cleared or grazed. The mining operation involves clear felling, then burning and removal of top soil. Subsequently the ore is blasted and heavy machinery used to remove it, leaving a pit on average 2 metres deep and at least a hectare in area. Efforts have been made to reclaim the mined areas by landscaping, replacing top soil, ripping the surface to enhance root penetration and revegetating by various methods. Different rehabilitation regimes are being tested to establish which is the most 'successful' in returning the mined area closest to its original state. Conventional botanical methods of monitoring the different treatments are being supplemented by studies of soil surface arthropods as they could provide additional information for assessing the different schemes. Luff and Hutson (1977) emphasise the benefits which originate from the soil fauna such as litter breakdown, and improvement of soil aeration. They stress that management of reclaimed land should aim to encourage development of the soil fauna. Here we describe the re-establishment of Collembolan populations in one set of rehabilitation trials and compare treatment populations with those of undisturbed forest. Results for ants have already been analysed (Majer in press).

SITES AND METHODS

The experimental plots were situated in the Darling Ranges about 80 km south of Perth at Del Park and Jarrahdale, where the predominate vegetation is tall closed forest of Eucalyptus marginata (jarrah) with some E. calophylla and an understory of Banksia grandis, Persoonia longifolia and Casuarina fraseriana. Three treatments were sampled:- U, an unplanted area where the only treatment was replacement of top soil and ripping; P, planted with seedlings of E. calophylla in June 1976 and spot fertilized, and S, treated as U but planted in July 1976 with a mixture of seeds and seedlings belonging to more than 20 species of Eucalyptus and Acacia and fertilised periodically. A control plot, F, of undisturbed forest was chosen nearby. Plots U and P were reclaimed with stockpiled topsoil at the same time and were adjacent to F; however the seeded plot was treated slightly differently with non-stockpiled topsoil, was reclaimed one month later and lay some 20 km north of the other plots, although on a similar soil and in similar vegetation. After two years both the U and P plots still consisted mainly of bare ground with a plant cover area of 0% and 15% respectively. No additional plants had succeeded in permanently colonising either plot although both were only about 200.m from the nearest source area. By the same time a dense cover of vegetation had developed on plot S and both plant area cover (73%) and plant density (14%) were greater than that of the forest control (70% and 2.6%). Some leaf litter was present on the ground surface on plot S after two years but it appeared to be lying loosely on top of firm textured soil; in contrast the forest soil was less compact and darker with a higher content of organic matter and more extensive litter layer.

Rainfall and temperature data for the area are given in figure 1. The climate is mediterranean with a hot, dry summer and cool, wet winter. Sampling was carried out with a grid 15 x 15 m of 36 (6 x 6) pitfall traps, 1.8 cm in diameter containing an alcohol/glycerol mixture as described by Majer (1978). The traps were operated for one week every month for the first year (June 1976 - July 1977) and thereafter four times a year. All Collembola trapped were counted but they were only identified from a selection of 8 samples which covered all seasons. Some disadvantages are implicit in using pitfall trap sampling alone since catches are dependant on the activity as well as the size of populations and influenced by density of surrounding vegetation and litter; however they were considered adequate for this survey for their convenience, speed and efficiency at collecting the groups to be studied so long as results were analysed with care. Most species of Collembola that were collected were undescribed, but all species were distinguished; numbered and voucher specimens are deposited in the South Australian Museum, Adelaide, South Australia.

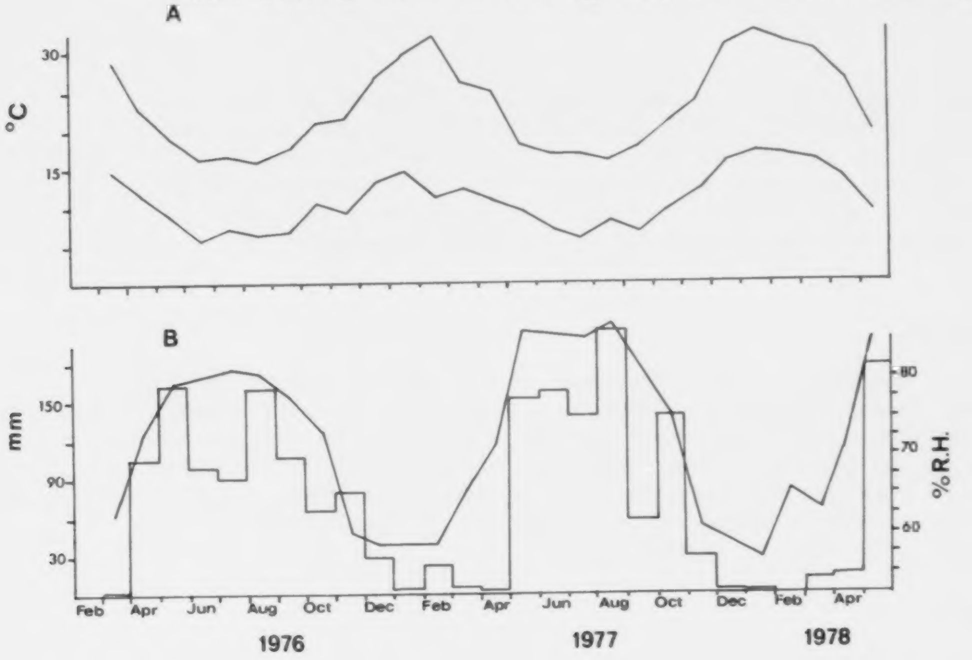
RESULTS

Abundance

Total numbers of Collembola trapped showed considerable variation between plots, and within plots between sampling occasions (fig. 2). At least part of these differences are accounted for by differing weather conditions on different sampling occasions. Overall the treated plots, in particular plot S, show greater variation in size of catch between sampling occasions than the forest control.

The following account refers only to the results from the eight sampling times indicated on figure 2 and are summarised in table 1. Catches from plots U and P are strictly comparable because of the physical similarity of their ground surfaces. The effect of the denser ground vegetation and litter on plots S and F would be to reduce activity and hence catches so that high catches here reflect a real increase in population density.

FIGURE 1. Climatic data from Dwellingup near experimental plots. A. Mean monthly maximum and minimum temperatures. B. Mean monthly rainfall (histogram), and relative humidity.



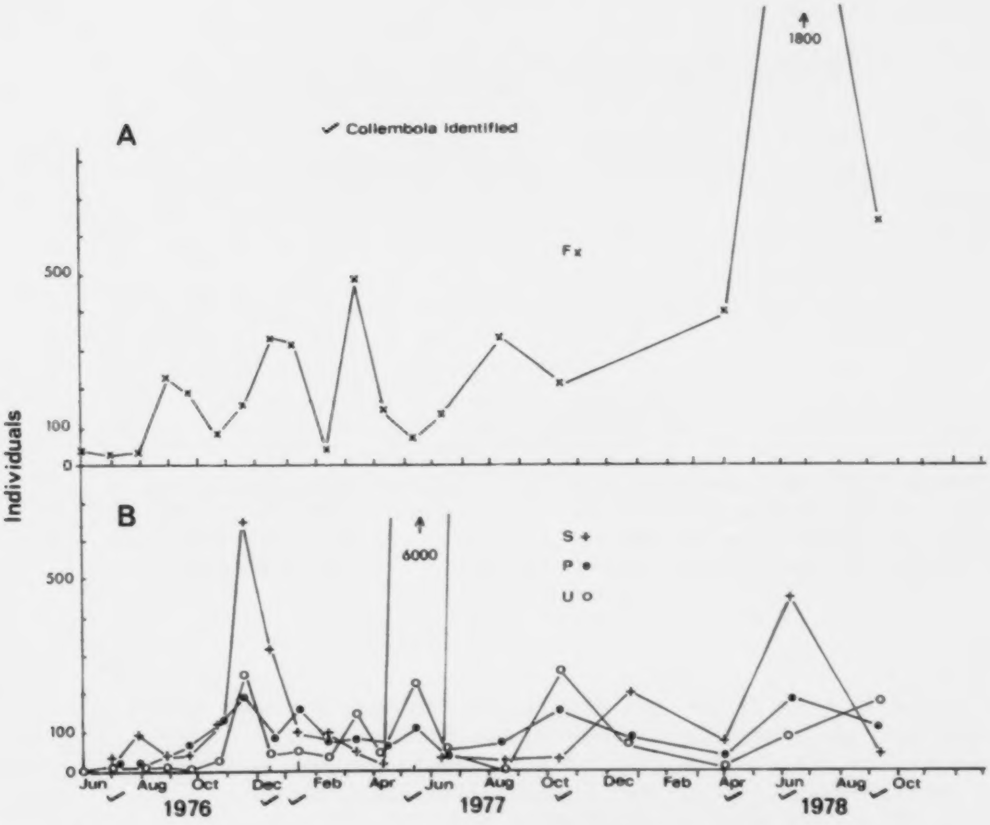


FIGURE 2. Total Collembola trapped June 1976 - September 1978: A, Forest control; B, Unplanted (U), Planted (P) and Seeded plots (S). ✓ - Samples from which Collembola were identified.

The total number of individuals trapped was highest on the seeded plot (S), (figure 3c), with catches 50% greater than those in forest. The planted and unplanted plots trapped few individuals. Biomass was not estimated but since the majority of individuals on F and particularly S were smaller than on U and P, biomass was more evenly distributed between plots than is indicated by catches of individuals.

Species Diversity

Diversity measured by the total numbers of species identified is highest in the forest control (F) (figure 3a) with the three treatment plots carrying about a third as many species. On both the planted and seeded plots (P and S) eighteen species were trapped. The differences are more marked when species records i.e. the sum of species occurrences are counted (figure 3b). Altogether 57 species were recorded from the four plots (table 1).

Faunal affinities

The species composition of the four plots was compared using the percentage similarity for each pair of habitats:-

$$\frac{\text{Number of shared species} \times 100}{\text{Total number of species in both habitats}}$$

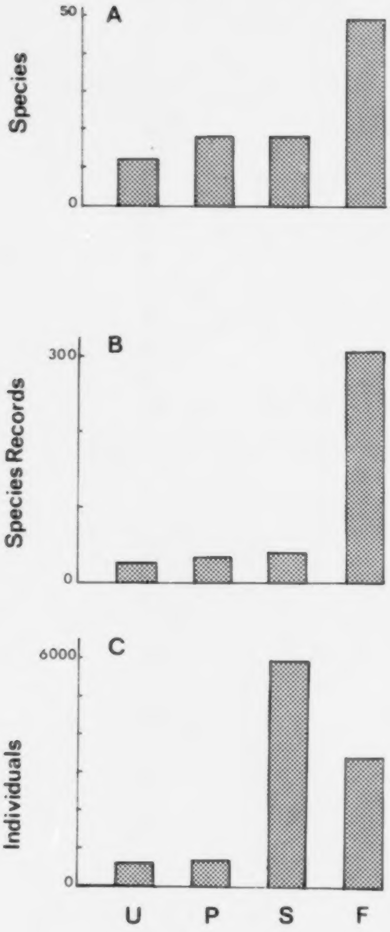
TABLE 2. Percentage similarity
U-Unplanted, P-Planted, S-Seeded, F-Forest

	U	P	S	F
U	-	45	22	16
P	-	-	30	25
S	-	-	-	32

The planted (P), and unplanted (U), plots showed most similarity to each other and the seeded plot (S) is slightly more similar to the forest control (F) than it is to the planted plot. As expected the plot least similar to the forest control is that of the bare ground (U).

Equitability

From figure 3 it is clear that plot S must contain a small number of species represented by a large number of individuals. In order to investigate the distribution of individuals between species, the species were grouped into octaves according to the number of individuals by which they were represented:-



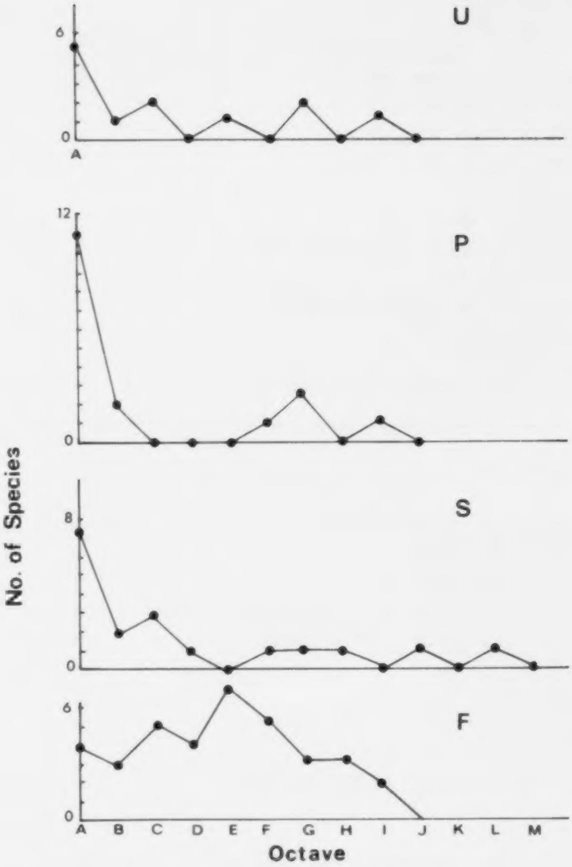


FIGURE 3. Combined data from eight sampling occasions. A, Total species recognised; B, Species records; C, Total individuals. Plots: U, unplanted; P, planted; S, seeded; F, forest.

FIGURE 4. Species grouped into octaves (A-M) according to number of individuals by which they are represented. Lognormal plot of species frequency distribution between octaves. Plots: U, unplanted; P, planted; S, seeded; F, forest.

TABLE 1. Number of Collembola species trapped on four plots on 8 sampling occasions.
Plots U-uplanted, P-planted, S-seeded, F-forest

Sminthuridae	U	P	S	F
Sminthurides sp. 1	-	-	≈200	6
Sminthurides sp. 2	-	59	8	
Sminthurides sp. 3	18	-	-	-
Imm indet. *Sminthurides*		-	-	-
Nr *Sminthurinus* sp.	6	2	13	82
Sminthurinus sp. 1	-	-	-	222
Sminthurinus sp. 2	7	92	81	32
Parakatianna sp.	-	-	2	5
Katianna sp.	-	3	1	39
Temeritas sp.	-	-	1	4
Aneuempodialis cinereus Wom.	1	-	-	7
Rastriopes sp.	-	1	5	16
Corynephoria cassida Wom.	-	-	-	1
Corynephoria sp.	-	-	-	6
Dicyrtomidae	-	-	-	3
Imm. indet. Sminthuridae	-	3	87	81

Entomobryidae	U	P	S	F
Lepidocyrtoides sp. 1	-	-	3	52
Lepidocyrtoides sp. 2	-	-	-	14
Lepidocyrtoides sp. 3	-	-	-	41
Lepidocyrtoides australicus Schott	-	1	-	-
Lepidosira coerulea Schott	-	-	-	162
Lepidobrya sp	-	-	-	330
Lepidosira sp.	-	-	-	
Drepanosira sp. 1	-	-	-	
Drepanosira sp. 2	-	-	-	22
Drepanura cinquelineata Wom.	1	2	61	13
Drepanura sp. 2	-	-	-	4
Drepanura sp.3	-	-	-	1
* *Entomobrya unostrigata* Stach	82	98	-	-
* *Entomobrya atrocincta* Schott.	1	2	-	-
Entomobrya sp.	-	3	-	1
Pseudosinella sp.	4	2	-	24
Acanthocyrtus sp.	73	80	513	113
Imm. indet. Entomobryidae	55	54	21	87

Table 1 (cont.)

Isotomidae	U	P	S	F	
Folsomides exiguus Folsom	-	-	-	1	
Folsomides sp.	-	-	-	7	
* *Proisotoma minuta* (Tullb.)	-	-	5000	-	
Proisotoma ripicola Linnaniemi sens Wom.	-	2	-	32	
Proisotoma sp.	-	-	-	22	
* *Cryptopygus thermophilus* (Axel.)	-	-	-	14	
Cryptopygus antarcticus Willem.	-	1	-	33	
* *Folsomia candida* (Willem)	-	1	-	-	
Acanthomurus sp.	415	314	7	314	
Proisotomurus sp.	-	-	-	49	
Isotoma sp. 1	-	-	1		
Isotoma sp. 2	-	-	-	130	
Onychiuridae					
* *Tullbergia krausbaueri* group	-	-	1	-	
Hypogastruridae					
Triacanthella sp.	1	-	3	155	
Neanuridae					
Xenyllodes sp. 1	-	-	-	+	>1100†
Xenyllodes sp. 2	-	-	-	+	
Zealandella sp. 1	-	-	-	++	
Zealandella sp. 2	-	-	-	++	
Zealandella sp. 3	-	-	-	++	
Subclavontella sp. 1	-	-	-	+++	
Subclavontella sp. 2	1	1	-	+++	
Subclavontella sp. 3	-	-	-	+++	
Nr. *Probrachystomella* sp.	-	-	-	+	
Australella sp. 1	-	1	2	+++	
Australella sp. 2	-	-	-	+++	
Pseudachorutes sp.	-	-	2	+++	
Total Species	12	18	18	49	

† These species were individually counted in all samples except that for June 1978 when the total was ≙ 1100 specimens for all Neanuridae. + = < 10 individuals; ++ = 11 - 100 individuals; +++ = > 101 individuals.

* Cosmopolitan species.

Octave A B C D E F G H I J K L M
No. of individuals 1-2-4-8-16-32-64-128-256-512-1024-2048-4096-8192

The data are plotted in figure 4. Plot F gives a truncated normal distribution with a large number of relatively abundant species. None of the treatment plots show a similar distribution pattern since individuals are inequitably distributed between species with a larger proportion of rare species and some very abundant ones. This is least obvious for plot U which has the least diverse fauna.

Species Composition

Species collected are listed in table 1. A number of species were only found on the treatment plots and these all have cosmopolitan distributions. Cosmopolitan species expressed as percentages of the whole fauna on each plot were: U, 17%; P, 17%; S, 11%; F, 0.4%. However 80% of individuals on the seeded plot were cosmopolitan and were identified as *Proisotoma minuta*, a species common on compost heaps and in other disturbed sites in Australia where humidities are high, food is plentiful and predation pressure is low, typical habitats for the *r* selected species of McArthur and Wilson (1961). *Proisotoma minuta* is able to increase in numbers rapidly when abundant food is present. Another cosmopolitan species, *Entomobrya unostrigata*, was abundant on plots U and P. This species is a relatively recent introduction to Australia and is often found in hot dry conditions on bare arable land and in houses. *Entomobrya atrocincta*, although rarer on these plots has the same recent history and characteristics in Australia.

On plot S, species associated with heath vegetation such as *Rastriopes* sp., *Parakatianna* sp. and *Drepanura cinquelineata* were present in fairly high numbers. These species did not occur on plots U and P and about half the number of individuals were trapped in the forest compared with the seeded plot. *Sminthurides* spp. were often abundant on the treatment plots in winter where small pits formed during ripping held puddles of water. The close similarity between plots U and P indicate that the effect of seedling trees, on species establishment was negligible. In fact only a single individual of a species which lives mainly under bark or on trees *Lepidocyrtoides australicus*, was trapped on plot P. Litter inhabiting Collembola such as Neanuridae, *Triacanthella*, *Cryptopygus*, *Isotoma*, *Sminthurinus*, *Lepidocyrtoides* and *Lepidosira* species were present only in the forest. Apart from those species discussed above the only species able to colonise the mined areas and maintain their populations were two native species: *Acanthomurus* sp., a large isotomid, and *Acanthocyrtus* sp. an entomobryid.

Seasonality

In spite of the variation between sampling occasions, figure 2 shows maximum catches in winter (May-August) and minimum in summer. The low number for winter 1977 is an artefact due to loss through flooding of traps. In both 1977 and 1978, the seasonal population increase began earlier in forest than mined areas and occurred simultaneously with increasing relative humidity, which was a result of falling temperatures in late March and early April. On the mined plots the first population increase was in May and coincides with the breaking rains of Autumn.

Bulked records of individuals trapped on the four plots, grouped seasonally are given in figure 5. No Neanuridae, Hypogastruridae or Isotomidae apart from Acanthomurus were trapped i.e. were active on the soil surface, in summer (figure 5e). There are two groups of Sminthuridae:- a) species mainly active in winter, and b) species mainly active in summer. Both were present in low numbers in spring and autumn. The Entomobryidae can also be classified into two groups:- c) species active predominately in summer, and d) aseasonal species with a peak of activity in the humid conditions of autumn before the winter fauna was abundant. Some species of Collembola were still trapped on all plots even during extremely dry conditions in summer when there is often no effective rain for > 4 months and temperatures are high.

Trends with time

Percent similarity of the faunas of treated plots and control are compared in table 3 for the results of spring trapping in 1977 and 1978. There was no increase over the year even on plots S where gross botanical changes had taken place.

TABLE 3. Percentage similarity of mined plots to forest on two occasions a year apart.
U - Unplanted, P - Planted, S - Seeded, F - Forest

		U	P	S
October 1977	F	21	18	23
September 1978	F	12	12	19

DISCUSSION

Reviews of other, mainly European work on the effects of mine reclamation on soil animals are given by Luff and Hutson (1977) and by Majer (in press). Three stages are involved in the development of a fauna on a virgin landscape:- 1) immigration, 2) population establishment 3) population maintenance. The first stage, requires species with dispersal ability. At least a third of the litter inhabiting species which occurred in forest were also found on the mined sites although frequently only single specimens were trapped. Hence dispersal does not seem to be a major obstacle to faunal development. For the second stage to be successful i.e. establishment of a population, food and appropriate habitat and shelter must be

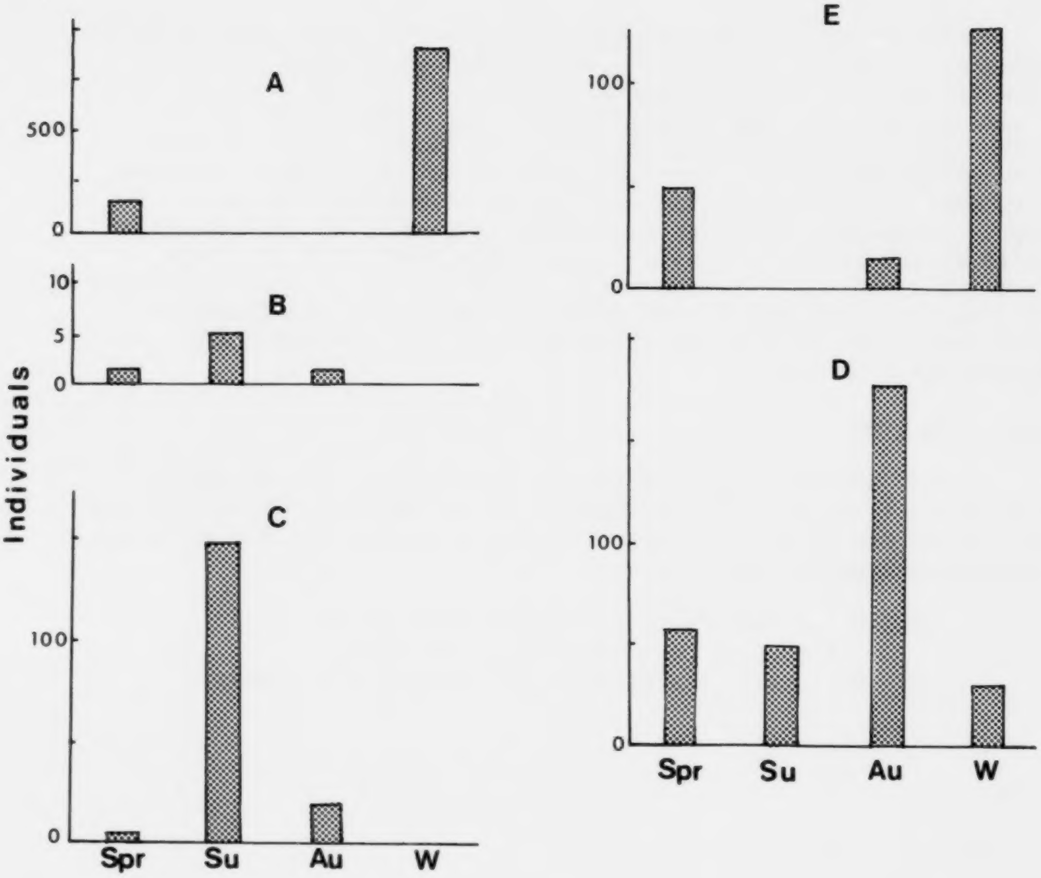


FIGURE 5. Seasonal occurrence of species. Spr - Spring (September - November); Su - Summer, (December - February); Au - Autumn, (March - May); W - Winter, (June - August). A. Sminthuridae Katiannini, Sminthuridinae, Temeritas sp. Total species 12. B. Sminthuridae Corynephoria sp. 2 spp. C. Entomobryidae Drepanura spp. Drepanosira sp. Entomobrya spp. Total 8 spp. D. Entomobryidae Acanthocyrtus sp. Lepidosira spp. Lepidocyrtoides spp. Lepidobrya sp. Total 8 spp. E. Isotomidae and Neanuridae. Total 25 spp.

available. This was not the case on the unplanted (U) and planted (P) plots and they did not support populations of common litter species. Although a litter layer was present on the seeded plot these litter species also failed to establish here. For the third stage, i.e. maintenance of population, the population which has established must be able to survive seasonal and short term variation in the environment. There was a relatively greater drop in number of species active in summer on mined plots (U and P) (10% active) compared to forest (F) (25%). This applied also on plot S with its dense shrub vegetation. It seems that the high temperatures and low humidities in leaf litter in summer do not permit many species to survive there.

Our results indicate that the Collembolan faunas of seeded, planted and unplanted plots were all markedly different from the forest fauna after two years reclamation, even though the seeded plot, because of the vegetation it carries, might be rated botanically 'successful'. The major group of Collembola missing from all these mined plots is the winter active species inhabiting litter. This includes all the Neanuridae as well as some species of Isotomidae and Sminthuridae. In the forest, the autumn population increase in total Collembolan catches occurs more than a month before the increase on the mined plots. It appears that an inactive population exists throughout the summer in forest which becomes active again as relative humidities increase in early autumn. On the mined plots, no increase in catches occurs before the breaking rains. We suggest that on the mined sites poor soil structure and low soil organic matter content limit the availability of refuges from harsh summer conditions. Even on plot S this seems to retard the development of a balanced Collembolan fauna.

These results for Collembola are similar to those recorded for ants (Majer in press), although the diversity of ants on plot S was relatively higher compared to the other plots than it was for Collembola. This probably results from the ability of many ant species to excavate their own refuges even in poorly structured soil.

From the point of view of the vegetation, reclamation of mined areas by seeding appears to be most effective. However, development of vegetation cover and a litter layer is not all that is needed for the recovery of the Collembolan fauna. Over the two year time scale of these observations, some heath species of Collembola reinvaded the seeded plot but none of the winter active litter inhabiting species typical of forest became re-established. These are the species most likely to contribute to decomposition and cycling of nutrients. We have suggested that soil structure may limit their occurrence. Future research could be directed towards examining this suggestion.

ACKNOWLEDGEMENTS

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QUESTIONS and COMMENTS

M.S. GHILAROV: Have you tried inoculating the mined sites with litter from the forest, to stimulate development of the fauna?

P. GREENSLADE: Not yet, but that technique would be interesting to try at some point in the research programme.

EARTHWORMS ON FORESTED SPOIL BANKS

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INTRODUCTION

Lands disturbed by surface mining are only slowly colonized by the larger saprophytic invertebrates (Neumann, 1973). Without these animals litter decomposition is slow (Edwards and Heath, 1963), and thick litter mats accumulate on the soil surface. Earthworms (Lumbricus terrestris, L.) can be introduced on stripmined spoil banks and help to increase the rate of litter decomposition (Vimmerstedt and Finney, 1973; Hamilton, 1979).

This is a report on the status and activity of an introduced population of L. terrestris on forested mine spoils in southeastern Ohio. One acre plantings of Alnus glutinosa and Robinia pseudoacacia were established in 1962 on spoil material rich in limestone and near neutral in reaction (Table 1). In May, 1967, 10 sexually mature L. terrestris were released in the approximate center of each plantation.

Table 1. SITE DESCRIPTION OF TWO FORESTED SPOIL BANKS

Site	Soil pH	mg NH_4-N/100 g Soil A	mg NH_4-N/100 g Soil B	Depth A-Horizon (cm)	Basal Area m^2/Hectare	g Woody Leaves per m^2 1/	g herbaceous leaves per m^2
Alnus	7.73	0.229	0.175	4.92	13.8 (Alnus) 0.69 (other)	129 ± 23.97	16.16 ± 9.84
Robinia	8.22	0.258	0.207	5.25	11.9 (Robinia) 0.1 (Other)	89.2 ± 6.83	26.08 ± 2.73

1/Woody and herbaceous leaf weights are fresh fallen leaves collected during October and November.

Work supported by McIntire-Stennis funds.

METHODS

In October, 1978 earthworms were sampled by chemical extraction with dilute formalin solutions applied to 32 0.25 m^2 plots (Raw, 1959). Each sample plot was twice extracted on consecutive days. Prior to extraction surface litter of each plot was carefully collected, oven-dried (at 80° C for 24 hours), and weighed.

Within 1 m of each extracted plot a second 0.25 m^2 plot was also cleared and the litter oven-dried and weighed.

Weekly collections of the fallen litter were made through October and November from plots which had been treated with formalin. Fallen litter on cleared unextracted plots was not disturbed. In March, 1979 both extracted and unextracted plots were cleared, and litter was oven-dried and weighed. Weight of leaf litter collected from plots devoid of worms represented 100% of litter fall for each plot pair. Weight of leaf litter collected from unextracted plots represented weight of leaves not acted on by worms. Initial clearing of plot pairs showed that the weights of leaf litter on each member of the pair were not significantly different.

Decomposition studies were conducted using a series of 1 gallon, glass, screw-top jars into which a uniform quantity of spoil (1.2 kg), leaves (3.85 g), and water (1/3 bar moisture, 26.7% HOH) were added. In some jars two active *L. terrestris* adults (combined weights from 7.5 to 9.1 g) were added. Leaf species were varied (*A. glutinosa* and *R. pseudoacacia*), and, in some jars, spoil and leaves were autoclaved (at 240° C for 2 hours). The autoclaving procedure was expected to reduce microbial numbers and open micro-niches, but not to completely sterilize the system. Table 2 indicates the 8 treatments.

Carbon dioxide evolution from litter and spoil was measured at 24 hour intervals. Titrations of an alkaline CO_2 absorbent (0.8 N NaOH) with 0.8 N HCl following saturation with $BaCl_2$ determined $mgCO_2 \cdot C$ evolved. Large jars and daily aerations insured the maintenance of aerobic conditions within the containers.

After 3 weeks of incubation at 16° C in the dark, spoil material was removed from the jars and 100 g sub-samples were treated with selective inhibitors (cycloheximide, 150 mg; streptomycin sulfate, 150 mg) and a carbon-energy source (glucose, 200 mg) in order to determine the bacteria to fungi ratio of each (Anderson and Domsch 1978a, 1978b). Amendments to subsamples were added dry and thoroughly mixed into spoil by hand. Samples were then incubated at 22° C, in the dark, for 8 hours in clean, 1 gallon, glass, screwtop jars with a beaker of alkaline CO_2 absorbent (0.2 N NaOH). The alkali was titrated against 0.5 N HCl after saturation with $BaCl_2$.

Table 2. RESULTS OF LITTER DECOMPOSITION STUDY: CO_2 EVOLUTION FROM A STANDARD SPOIL-LITTER SYSTEM.[1] MEASURED BY STATIC CO_2 ABSORPTION SYSTEM OVER 21 DAYS.

Treatment	Cumulative mg CO_2-C per Jar	% Weight Loss of Litter	% Weight Gain by Worms	Relative Fungi on Litter[4]
A. glutinosa leaves, earthworms[2]	60.78 ± (1.66)[5]	54.7 ± (1.61)	21.8 ± (2.23)	0
A. glutinosa leaves	48.39 ± (2.18)	19.3 ± (3.26)	———	+++
A. glutinosa leaves, autoclaved,[3] earthworms	49.56 ±(3.71)	38.0 ± (3.71	10.0 ± (2.55)	++
A. glutinosa leaves, autoclaved	28.86 ±(0.45)	11.2 ± (1.03)	———	++++
R. pseudoacacia leaflets, earthworms	51.67 ±(1.42)	41.6 ± (5.59)	4.8 (2.38)	0
R. pseudoacacia leaflets	40.89 ±(1.10)	8.1 ± (0.80)	———	0
R. pseudoacacia leaflets, autoclaved, earthworms	46.32 ±(1.89)	9.1 ± (4.47)	3.8 ± (3.75)	0
R. pseudoacacia leaflets, autoclaved	27.45 ±(1.37)	5.2 ± (0.58)	———	+++

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[1] 1.2 kg spoil, 3.85 g leaf tissue; spoil brought to 1/3 bar moisture (26.7% HOH); in 1 gallon, glass, screw-top jars incubated at 16° C in the dark.

[2] 7.5 to 9.1 g combined weight, 2 adult *L. terrestris* per jar.

[3] "Autoclaved": both the 1.2 kg spoil and the 3.85 g leaf tissue were autoclaved at 240° C for 2 hours.

[4] Measured as relative surface area of leaves with fungal growth.

[5] Numbers in parenthesis indicate standard error.

RESULTS AND DISCUSSION

Sampling within each plantation and in immediately surrounding areas in October, 1979 showed that after 12 years the introduced *L. terrestris* had successfully multiplied and had dispersed throughout their respective woodlots. The worms had not, however, colonized the surrounding, non-wooded areas. Also no evidence of invasion of *L. terrestris* from outside the study area was observed.

Under *A. glutinosa*, *L. terrestris* reached a significantly greater biomass per m^2 (164.26 vs 60.00 g fresh wt/m^2), and buried leaf litter to a greater degree over a six month period (91.7 vs 43.0%) than under *Robinia psuedoacacia* (Table 3). This preference for *A. glutinosa* leaves compared to *R. pseudoacacia* leaflets was also reflected in the incubation experiments where unautoclaved *A. glutinosa* treatments with earthworms produced significantly greater amounts of CO_2 over a 3 week period than comparable treatments with *R. pseudoacacia* leaflets (Tables 3, 4). Worms feeding on *A. glutinosa* leaves also showed significantly greater weight gains than worms which fed on *R. pseudoacacia* leaflets (Table 3). *A. glutinosa* leaves are a highly preferred leaf by *L. terrestris*, (Satchell and Lowe, 1967) and have a high food caloric value (Bocock, 1964). *R. pseudoacacia* leaflets, however, contain phytotoxic compounds and cardiac glucosides (Hardin, 1962), substances which may make leaf tissue less palatable to worms.

Table 3. EARTHWORM (*L.TERRESTRIS*) POPULATIONS ON TWO FORESTED SPOIL BANKS AND THE PERCENT OF WOODY LEAF LITTER REMOVED OVER A SIX MONTH PERIOD, OCTOBER 1978 - MARCH 1979

Site	# Adult Worms per m^2	g Adult Worms per m^2	Mean Wt. Adult Worms	% Leaf Litter Removed[1]
A. glutinosa	56.5**	164.26**	3.03*	91.7*
R. pseudoacacia	27.52**	60.00**	2.12*	43.0*

**sig to p $\leq$.001

*sig to p $\leq$.01

[1] Determined by paired plots, one of which had worms while in the other worms were removed with formalin.

Reynolds (1972) noticed low earthworm numbers under *R. pseudoacacia* stands in Indiana. He felt that the worm populations were inhibited because rapid microbial decomposition of *R. pseudoacacia* leaflets was moving leaf carbon directly into humus carbon, thus decreasing the amount of food available to leaf-feeding worms. Observations, however, in this paper showed that over a 21 day incubation period, A. glutinosa leaves (which in the field supported a high density of worms) decomposed more rapidly than R. pseudoacacia leaflets (Table 2). Presence of chemicals antagonistic to the worms in the R. pseudoacacia leaflets seems a more logical explanation for the low earthworm numbers.

There was greater observed fungal growth on A. glutinosa leaves (Table 2), and a tendency for higher soil fungal percentages (Table 4) in treatments with A. glutinosa litter. Possibly, this reflects the lack of inhibitory substances in A. glutinosa leaf tissue.

Table 4. BACTERIA, FUNGI RATIO (B/F) AND RELATIVE MICROBIAL ACTIVITY IN SPOIL MATERIAL AFTER 4 WEEKS OF INCUBATION WITH VARIOUS TREATMENTS

Treatment	B/F[2]	Relative M/O Activity[3]
Spoil, A. glutinosa leaves, earthworms	40/60	15.39
Spoil, A. glutinosa leaves	70/30	6.28
Autoclaved[1] spoil, autoclaved A. glutinosa leaves, earthworms	45/55	16.79
Autoclaved spoil, autoclaved A. glutinosa leaves	30/70	12.59
Spoil, R. pseudoacacia leaflets, earthworms	40/60	12.59
Spoil, R. pseudoacacia leaflets	40/60	7.68
Autoclaved spoil, R. pseudoacacia leaflets, earthworms	60/40	18.19
Autoclaved spoil, R. pseudoacacia leaflets	90/10	10.48

[1] "Autoclaved", both the spoil material and the leaves were autoclaved at 240° C for 2 hours.

[2] Bacteria/fungi ratio of relative activities as measured during 8 hour incubation after specific inhibition. Rounded to nearest 5%.

[3] Relative 8 hour production of CO_2C after the addition of 200 mg glucose to 100 g of soil.

Differences in $CO_2\cdot C$ evolved per jar between autoclaved samples with worms and autoclaved samples without worms (21 mg $CO_2\cdot C$ for *A. glutinosa*, and 19 mg $CO_2\cdot C$ for *R. pseudoacacia*) are greater than differences between unautoclaved samples with worms and unautoclaved samples without worms (12 mg $CO_2\cdot C$ for *A. glutinosa*, and 10 mg $CO_2\cdot C$ for R. *pseudoacacia*) (Table 5, Fig. 1). This difference either represents colonization of autoclaved systems with intestinal microorganisms from the earthworms, or accelerated growth, as a consequence of actions of worms, of those microbes which survived autoclaving procedures.

Table 5. ANALYSIS OF VARIANCE OF CO_2 PRODUCTION FROM LITTER ON SPOIL MATERIAL AFTER VARIOUS TREATMENTS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	Significance
Leaf species[1]	1	264.87	264.87	17.4	0.005
Worms[2]	1	2405.45	2405.45	158.05	0.005
Autoclaving[3]	1	1489.74	1489.74	97.89	0.005
Species of leaf x autoclaving	1	78.38	78.38	5.15	0.05
Species of leaf x worms	1	3.85	3.85	<1	----
Autoclaving x worms	1	182.88	182.88	12.01	0.005
Species of leaf x autoclaving x worms	1	1.37	1.37	<1	----
Error	31	471.79	15.2190		
Total	38	4898.33			

[1] Either *A. glutinosa* or *R. pseudoacacia*.

[2] Either worms (*L. terrestris*) were present or not.

[3] "Autoclaving" = both the leaves and the spoil were autoclaved. at 240° C for 2 hours.

The greatest soil microbial activity, measured as $CO_2\cdot C$ evolved over 8 hours after adding 200 mg glucose to 100 g spoil, was observed in autoclaved treatments with worms. The least soil microbial activity was observed in unautoclaved treatments without worms. Possibly, the

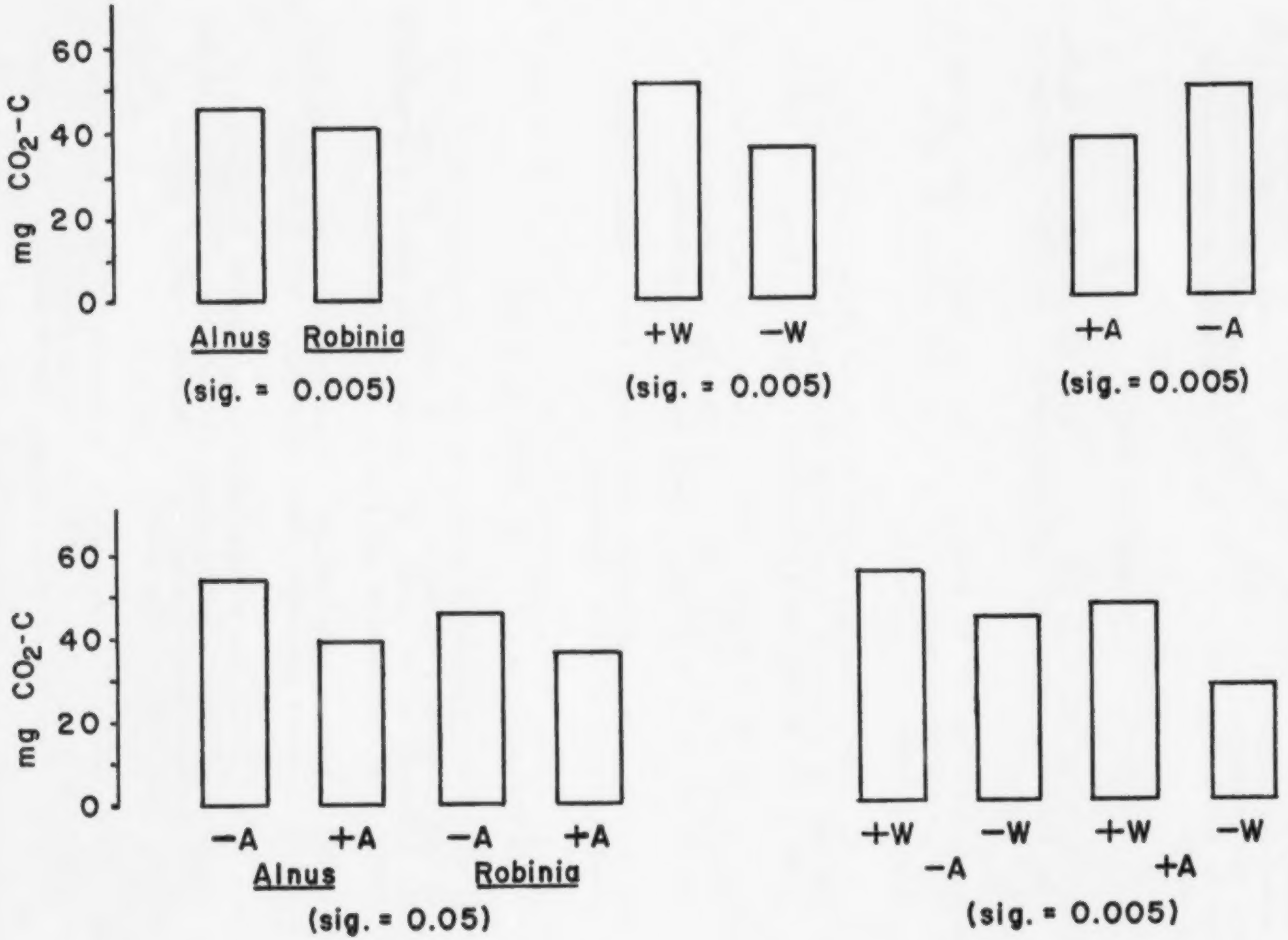

Figure I: RESULTS OF ANALYSIS OF VARIANCE IN DECOMPOSITION STUDY
Abbreviations: W (worms), A (autoclaving)

former represents an opened microbial system being colonized by rapidly metabolizing, opportunistic organisms (either from worms' intestines or as a consequence of actions of worms), while the latter represents a more slowly metabolizing, equilibrium population of microorganisms. A more exact determination and quantification of both soil microbial populations and intestinal microflora of worms is needed to determine whether or not active "seeding" of microbes by worms is occurring in these systems.

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QUESTIONS and COMMENTS

K. RICHTER: Can nutritional content of Alder i.e., calories and/or chemical composition account for the differences in preference between A. glutinosa and R. pseudoacacia rather than phenolic compounds?

Are you aware of any chemical changes with respect to phenolics and senescence in R. pseudoacacia i.e. are secondary substances reabsorbed, broken down etc. prior to leaf abcision?

W. HAMILTON: Alnus leaves are known to be high in calories and sugars and are highly preferred by L. terrestris. Whether the difference in preference by L. terrestris for Alnus and Robinia is due to a high preference for Alnus on a rejection of Robinia could not be answered absolutely in this experiment.

I am not aware that that occurs. It is my understanding that there are, indeed, phenolic compounds in the freshly fallen Robinia leaflets.

J.E. SATCHELL: Do you think the greater stimulation of microbial activity obtained in your autoclaved leaves could have been due to nutrient mobilization by the autoclaving? Perhaps this could be clarified in an experiment using irradiated litter.

W.E. HAMILTON: The autoclaving is a very severe physical manipulation, and I am sure that it did have an impact on the physical and chemical properties of the leaves. Perhaps an alternative method of "sterilization" could be employed.

S.E-D. A. FAIZY: Will you please give some reasons for the strikingly large variation (from <1 to 9) in the Bacteria/ Fungi) ratio with different treatment?

W.E. HAMILTON: The only general statement I have been able to make concerning the B:F ratio data is that there appears to be a greater relative activity of fungi in the Alnus treatments. I do not think it unusual, however, to observe very different B:F ratios in soil samples which have undergone such a variety of treatment manipulations.

SESSION VI: EFFECTS OF SILVICULTURAL PRACTICES ON SOIL ORGANISMS

Moderator: Veikko Huhta

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THE EFFECTS OF HARVESTING PRACTICES ON ORIBATID MITES AND MINERAL CYCLING IN A SITKA SPRUCE FOREST SOIL

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INTRODUCTION

In Britain, commercial forestry is concentrated in the wet, infertile uplands of Scotland and North Wales. Large-scale afforestation of these areas, previously used for grazing or arable land, is relatively recent. The first planting began in the 1920's, although the major surge of planting occurred in the 1950's. These primary plantations are presently being harvested and the second rotation established. Work in progress by the Forestry Commission, the Macaulay Institute for Soil Research, Institute of Terrestrial Ecology and various university departments may provide some indication as to the effects of various felling practices on both the physical and biological properties of these phosphorus-deficient and, for most of the year, anaerobic forest soils.

Recently, whole tree harvesting (removal of most of the tree including normal forest residues) has been suggested for the future in order to maximize yield. Such a practice will result in considerable nutrient removal from the site (in branches, needles, boles, for example) as well as initiating a changed pattern of soil damage. The absence of 'lop and top' will expose the soil surface to considerable weathering and possible erosion.

Within the Forestry Commission's objectives of determining both short-and long-term effects of harvesting practices on the establishment, long-term success and management of the second rotation, this paper is designed to outline certain microenvironmental changes brought about as a result of two contrasting felling practices; standard clear-felling and whole tree harvesting. Concomitant changes in species composition and diversity of the oribatid mite component of the soil fauna are being monitored, and some preliminary results are presented. The possible functional significance of such changes on such long-term processes as mineral cycling are discussed.

SITE DESCRIPTION; MATERIALS AND METHODS

The study site is situated in Beddgelert forest in the Snowdonia National Park, North Wales (S.H. 5659, altitude 300-380m). The soil type is a peaty gley with dispersed iron pan, the surface peat layer being approximately 25-30 cm thick. The pH of this layer varies between 2.8 and 3.8 and decreases with depth. Before felling, the crop was Sitka spruce, planted at 1.4 m square spacing with a maximum annual increment of 12 $m^2.ha^{-1}.yr^{-1}$. The crop was planted in 1930 and was clear-felled by sky lining in June 1978.

Two experimental plots, 80m x 80,, within the harvested area, were marked and staked with an intervening buffer zone of 10-15m. One plot was left untreated with none of the felling debris removed; this plot is termed CF. It has very little, or no, ground vegetation but a cover, varying between 50cm and 1m deep, of felling debris, branches, twigs and needles. The other plot was cleared of all felling debris except large discarded trunks. This plot is intended to simulate a complete or 'whole tree' harvesting practice, and is termed WTH. Finally, a control plot (C), 80m x 80m, was established in an adjacent forest stand. The soil and tree conditions almost exactly reproduce those of the two experimental plots prior to felling.

Sampling and measurements

Samples are taken at three to four month intervals beginning in June 1978. A regular sampling program has been disrupted by bad weather but results have been obtained for June 1978, November 1978, January 1979, March 1979 and July 1979. On each sampling occasion, 14 cores ($16.3\ cm^2 \times 5.5\ cm$), seven from the combined litter and fermentation layer and seven from the humus layer, are taken along a transect line in each site. Oribatid mites are extracted from the samples using Kempson bowl extractors. Additional samples of the humus layer are taken for measurement of pH, moisture content, organic content and bulk density from each site on each sampling occasion. These parameters outline the effective environment of the soil system. They describe the amount of living space and indicate the availability of food. Changes in pH may be directly attributable to changes in carbon dioxide levels and thus may provide an indicator of community metabolism.

A 12 hour temperature profile is recorded in the surface litter, sub-surface litter and humus at each site and on each sampling occasion.

Atomic absorption spectroscopy

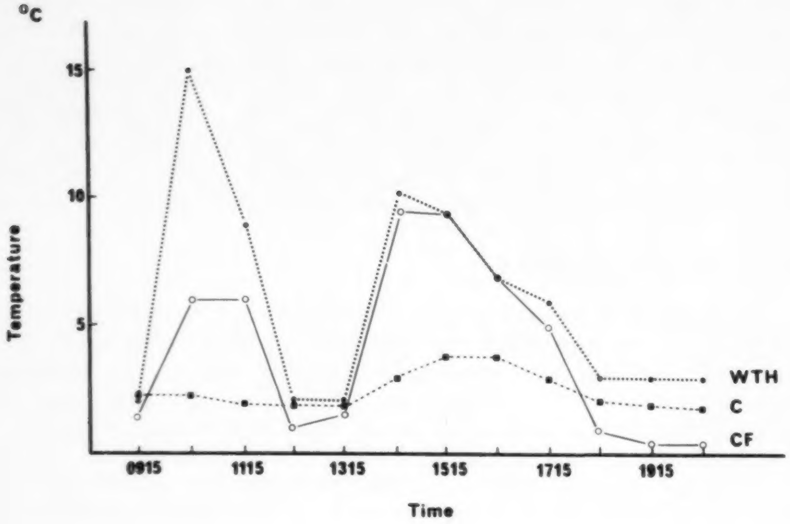
Calcium analysis of two mite species has been undertaken using A.A.S. Preliminary results are presented.

RESULTS

Temperature

Figure 1 shows the variations in litter temperature over a 12 hour period at each of the three sites during March 1979 sampling. These curves are typical of those obtained on other sampling occasions. Clearly there are distinct differences between the control plot and the two experimental plots which appear directly attributable to harvesting practice. Removal of both canopy and felling debris in WTH produces wide fluctuations in temperature. Increases of up to 15°C were recorded within one hour in the litter layer of this plot, compared with a maximum variation of only 1 or 2°C in the control plot. These fluctuations are dampened to a certain extent by the presence of a surface cover of felling debris in the CF plot, although variations of up to 9.5°C within one hour were recorded here.

FIGURE 1. Variation in litter temperature over a 12 hour period during March 1979 in each of the three sampling sites (C = control; CF = clear-felled; WTH = whole tree harvested).



Moisture content

Data on moisture content, expressed as % of fresh weight, are given in Table 1.

TABLE 1. Moisture content (%) of samples from H layer in each of the three sampling sites. Values are means of eight subsamples.

Sampling occasion	Sampling sites		
	C	CF	WTH
June 1978	84.6	84.3	21.7
November 1978	82.5	52.8	32.0
January 1979	82.5	80.4	56.0
March 1979	68.4	75.6	61.2
July 1979	71.0	75.0	62.3

These values indicate considerable drying out in WTH, particularly as an immediate effect after the felling period. Felling debris in CF and the presence of a closed canopy in the control obviously afford considerable protection and reduce evapotranspiration, although the variable nature of the CF values may, in part, indicate the patchy debris cover in parts of this site. The moisture content in WTH increases over the last three sampling times and this is directly attributed to the development of herbaceous vegetation in this plot, consolidating the ground surface and preventing excess water loss from the site.

pH

Data on pH of the humus layer at each site are given in Table 2.

TABLE 2. pH values of samples from humus layers in each site, measured in 0.01M $CaCl_2$ at 1:20 W/V suspension (means of four subsamples).

Sampling occasion	Sampling sites		
	C	CF	WTH
June 1978	3.65	3.65	4.05
November 1978	3.50	3.58	4.45
January 1979	3.20	3.00	3.70
March 1979	3.40	3.05	3.65
July 1979	3.60	3.30	3.90

It may be noted that WTH sustains a higher pH value than the other two sites throughout the period, although the difference is certainly being reduced in the last two sampling occasions. This initial increase in pH in WTH may be the result of an initial loss of organic material from the soil (see below). It is interesting to note in passing that Sundman, Huhta and Niemela (1978) recorded a rise in bacterial numbers immediately after harvesting in a spruce forest, and this may have been a response to a soil pH increase such as has been found here. The tendency of pH values in WTH to come closer to those of the control on later sampling occasions may indicate a reversion to a steady state after an initial change in the activity of the soil system.

Loss on ignition

Data for loss of weight on ignition of the humus layers from each of the sites indicate a decline of up to 30% in WTH compared with the control and CF plots immediately after felling. This is possibly due to erosion of organic layers as well as the removal of organic input in WTH. This is further reflected in bulk density measurements of the organic layer of the three sites. Dragging effects of the WTH simulation appear to have loosened the soil, increased the bulk density and therefore the living space, whilst reducing the organic content, and therefore food availability.

Species composition and diversity

Table 3 shows the total numbers of oribatids, total numbers of species and the equitability components for each site on the first three sampling occasions. Data for the later samplings have not yet been analysed.

TABLE 3. Total numbers of individuals (N), species (S) and equitability components (e) of oribatid mites in each of the sampling sites on three sampling occasions (14 cores per site).

	June 1978			November 1978			January 1979		
	C	CF	WTH	C	CF	WTH	C	CF	WTH
N	476	632	226	337	531	316	1061	833	512
S	15	19	13	16	16	18	19	17	14
e	0.66	0.39	0.69	0.84	0.44	0.65	0.55	0.73	0.89

It is interesting to note that there are considerably fewer individuals in WTH than in the control and CF plots on all three sampling occasions, but particularly in June 1978. The number of species is also lowest in WTH at this time, although the number of species does not alter significantly between plots or between sampling occasions. On the other hand, appreciably higher numbers of individuals are recorded from CF, compared with the control on the first two sampling occasions, although this contrast does not occur on the third sampling occasion.

An examination of equitability components for the first two sampling occasions may provide an interesting interpretation of these results. In WTH equitability is relatively high in June 1978, hardly departing at all from that shown by the control. In November 1978, equitability remains at the same level as in the previous June in WTH but has increased in the control. However, in CF the equitability is considerably lower than either the control or WTH on both sampling occasions, indicating that a change in species composition has occurred in this site.

The two harvesting practices, clear-felling and whole tree harvesting have quite distinct and immediate impacts on the soil environment. The initial effects of whole tree harvesting are physical, or mechanical, and as far as the oribatid fauna is concerned there appears to have been an indiscriminate reduction of individuals, irrespective of species. This effect can be attributed directly to the removal of surface organic material and considerable mechanical disturbance in the site. Further evidence for this is provided by the complete absence of Platynothrus peltifer (C.L.K.) from WTH in June 1978 and by a lower number of individuals of many other litter-dwelling oribatid species. In addition, Malaconothrus punctatus (v.d. Hammen) which was present initially in the control and CF plots becomes considerably reduced in WTH. This species prefers wet biotopes, and its low numbers in WTH may be a reaction to the drier conditions prevailing here. Such changes in species composition would not necessarily change the equitability value, since this statistic gives a measure of the apportioning of individuals among available species, rather than the absolute numbers of species and individuals.

By contrast, changes occurring in CF are characterised by population increases in certain opportunisitic or exploitive species. P. peltifer, Oppia quadricarinata (Mich.), Suctobelbella vera (Moritz) and Oppia obsoleta (Paoli) in June 1978, and Phthiracarus affinis (Hull) in November 1978 are present in considerably higher numbers in CF compared with the control. The immediate effect of clear-felling is to increase the organic input, in the form of 'lop and top' into the soil. This is a biological effect, sharply in contrast with the physical effects produced in WTH. This increased organic input may favour a selective group of litter-dwelling species, particularly those which feed on needles, such as P. affinis. The shifting balance of populations in favour of such species could account for the low equitability levels observed in CF on the first two sampling occasions.

The data for January 1979 are more difficult to interpret. There are some indications that the initial shock to the soil system occasioned by the harvesting practices may now be becoming attenuated. Numbers of individuals increase in all sites, although this may be due to an intrinsic seasonal cycle. As already mentioned, there are no significant differences between the numbers of species present, compared with the two previous sampling occasions, but the equitability values have changed quite considerably from those obtained in November 1978. The value for the control is now approximating that obtained in June 1978 and, perhaps, this is indicative of a seasonal cycle. Equitability in CF has now risen well beyond its earlier values and, again is approaching that of the control, possibly indicating that some measure of environmental stability is being achieved. In WTH, equitability rises to a surprisingly high level in January 1979. There is no obvious explanation for this increase, although it should be noted that the character of this site has changed considerably from its original condition with the development of a herbaceous ground layer. Such a transition from forest to a more open grassland type is likely to produce a reduction in the numbers of oribatid species and, maybe also, a more equitable redistribution of individuals among the remaining species. Data from subsequent sampling should clarify this situation.

Calcium analysis

The identification of shifts in species dominance and diversity is not merely of academic interest in nutrient-deficient sites, such as the one studied here. Oribatid mites vary in their roles as potential reservoirs of available mineral elements. The calcium contents of two species have been analysed by atomic absorption spectroscopy, and the results obtained illustrate this point adequately.

The two species in question are Phthiracarus affinis and Platynothrus peltifer, and the mean values for calcium content, in ppm, are given below:

P. affinis	P. peltifer
$\bar{x} = 1489.6$	$\bar{x} = 112.8$

It is evident that P. affinis consistently shows a higher calcium content than P. peltifer by a factor of 14 or 15. Both have relatively low values, as would be expected in such highly acid soils. This analytical approach will be extended to other species occurring in the sites in due course.

CONCLUSIONS

1. Felling practices, particularly whole tree harvesting, have immediate, short-term effects on temperature, moisture and pH regimes in forest soils.

2. These effects are reflected in changes in species composition and diversity of oribatid mites.

3. Short-term physical, or mechanical, effects are particularly evident after whole tree harvesting where a reduction of individuals has occurred without a change in species composition or diversity. A different effect is evident in the clear-felled plot where a restricted number of opportunistic species may have benefited from the increased organic input.

4. Long-term effects are only just becoming apparent and these seem to involve a recovery from the harvesting perturbation in the clear-felled site. Changes in species' abundance in the whole tree harvest site may be associated with the development of a ground layer of herbaceous vegetation.

5. Species of oribatid mites differ in their ability to concentrate such elements as calcium. This fact is being used to interpret the significance of changes in abundance and diversity of the oribatid fauna in the context of mineral cycling in the harvested plots.

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ASSESSMENT OF TOXIC EFFECTS OF THE HERBICIDE 2, 4, 5-T ON THE SOIL FAUNA BY LABORATORY TESTS

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Introduction

During the past decades it has become clear that the environmental risk of new synthetic chemicals has to be assessed before introducing these chemicals into the environment. This holds especially for pesticides, since these are developed to kill animals or plants. And although these pesticides are meant to be selective, numerous examples of environmental side effects show that this is not always true. For this reason suitable risk assessment methods should be developed. To find out the risks involved in the application of new pesticides field plots can be sampled regularly before and after a treatment. Alternatively in the laboratory a number of selected species can be tested for their sensitivity for pesticides. Laboratory research has the advantages of speed, low cost, relative simplicity and controlled environmental conditions. However, because of this simplicity numerous relationships between the species under study and other members of the soil fauna have to be neglected. Moreover, laboratory conditions have to be selected and fixed contrarily to the locally and temporarily fluctuating conditions in the field.

In this study it is tried to meet these discrepancies. Therefore, ways have been analyzed in which soil fauna species get into contact with the herbicide 2,4,5-T. 2,4,5-T has been widely used in forestry. In The Netherlands it has been applied in forests and nature reserves to control black cherry (Prunus serotina Ehrh.). In recent years there is a growing concern about the toxicity of this compound for non-target organisms, but little information is available on the fauna exposed to the herbicide. Because a large part of the herbicide reaches the ground either directly during spraying or indirectly after leaf-fall of sprayed Prunus shrubs, possible effects on the soil fauna are of special concern.

Therefore in the laboratory experiments about effects of 2,4,5-T by direct contact have been done with 14 soil fauna species to evaluate their relative sensitivity. With three of these species, representing different functional soil fauna groups, further experiments have been carried out concerning the way the mobility and food consumption of the animals are influenced by the herbicide. Furthermore, the effect of changing and constant environmental conditions (temperature and moisture) on the herbicide's impact has been studied.

Materials and methods

For the experiments animals were collected freshly from the litter of a forest next to the Institute with the aid of Tullgrens funnels and pitfalls or by hand sorting. They were stored in the laboratory on a moist soil substrate in the dark at 15°C for a maximum period of three weeks. The animals were fed regularly.

The experiments about the effects of direct contact with the herbicides were carried out in glass dishes (Ø 9 cm) or refrigerator boxes (20 x 20 c with a substrate of moist sifted sand (1 mm mesh.). Substrate and animals were sprayed with a spraying apparatus adapted from Ten Houten and Kraak (1949).

Food consumption experiments were carried out in small glass or plastic dishes (Ø respectively 5 and 2 cm). The different food items were sprayed with the herbicide or soaked in it in a partial vacuum. The amount of food consumed was measured as food weight loss or pellet production. The amounts of herbicide in the soil substrate and the different food items were analyzed by gas chromatography. All experiments were carried out in climate rooms at 15°C and 90% RH. For full details about the set up of the different experiments and the chemical analysis the reader is referred to Eijsackers (1978 a, b, c and d).

Results

1. Possible ways of uptake and effects of 2,4,5-T on mortality.

The effects of 2,4,5-T on the longevity of 2 isopod species, 1 millipede, 4 collembole and 7 carabid species after spraying 0.3, 1.25 and 5% aqueous solutions of 2,4,5-T on the animals and the soil substrate are summarized in table 1. Spraying of a 5% solution causes with all the species a decreased longevity, which varied from 5% up to a 20 fold decrease. This variability exists both within and between the different soil fauna groups. The more sensitive species also show a distinct decrease after treatment with a 1.25% and even with an 0.3% solution of 2,4,5-T. The species selected for further experimentation do show a more or less medium sensitivity. The selected species were the isopod *Philoscia muscorum* Scopoli representing the primary decomposers; the collembole *Onychiurus quadriocellatus* Gisin representing the secondary decomposers and the carabid *Notiophilus biguttatus* Latr. as a predator. The different ways these species can contact 2,4,5-T,

Table 1. Longevity relative to untreated specimen of isopod, millepede, collembole and carabid species after treatment with different doses of 2,4,5-T.

Species	Concentration of 2,4,5-T 0.3%	 1.25%	 5%
ISOPODS			
Philoscia muscorum	*0	-	--
Oniscus asellus	-	-	-
MILLIPEDES			
Glomeris marginata			-
COLLEMBOLES			
Onychiurus quadriocellatus	0	-	--
Tomocerus flavescens	-	--	--
Tomocerus minor	-	--	--
Orchesella cincta			--
CARABIDS			
Abax ater		0	-
Abax parallelis	+	+	--
Nebria brevicollis	0	-	-
Pterostichus oblongopunctatus	+	-	--
Asaphidion flavipes	+	+	
Leistus rufomarginatus	-	--	--
Notiophilus biguttatus	-	-	--

*0 no or hardly any difference in longevity with control

-/+ decrease/increase of longevity of 5-90%

-- decrease of longevity with a factor 2-20 (e.g. from 40 to 20, resp. 2d.)

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are shown in Fig. 1. The 2,4,5-T solution drifting away during spraying and dripping of the leaves afterwards has an irregular distribution on the forest floor (Table 2). Because of this irregular distribution and the distribution of the soil fauna and its mobility, it is not only necessary to establish the effects under continuous exposure with a completely treated substrate, but also on a partly treated substrate. In this situation it is important whether the animals are able to distinguish treated from untreated areas of the substrate.

2. Impact of the mobility of the animal on the effect of the herbicide.

To study the behaviour of the animals, individual specimens were observed directly during 10 minutes after entering a box with a partly treated substrate. When entering and making a first choice between the treated and untreated part of the substrate (Fig. 2) neither the isopod nor the carabid showed an avoidance of the treated part. The isopod even preferred the substrate sprayed with a low dose of 2,4,5-T compared to the control experiment in which extra water was sprayed as a treatment. However, the springtail clearly avoided the part treated with the herbicide. Comparing the distribution of the residence times in the treated and untreated parts of control, low dose and high dose experiments (Fig. 3), there was made again no significant distinction by isopod and carabid whereas the collembole showed a distinct repellent reaction, consequently they were able to avoid or withdraw from a treated area. To evaluate this avoidance over a longer period, experiments were also done during which the animals were observed once a day during a 30-day period. From figure 4 it becomes clear that the carabid still did not show any avoidance, but the isopod and the collembole avoided the treated area. Notwithstanding this avoidance, the isopod and collembole have an increased mortality on the substrate partly treated with a 1.25% solution of 2,4,5-T. This increased mortality also holds for the carabid. Comparing the mortality of continuously exposed animals and animals with a temporary exposure on a partly treated substrate (Table 3) it is clear that the possibility to avoid or to withdraw from treated areas of a soil substrate diminishes the mortality of isopod, collembole and carabid.

3. The effect of the herbicide via food consumption

Saprophagous soil fauna plays an important role in litter break-down.

Table 2. Distribution of 2,4,5-T (0.001 ml/dm^{2*}) on the forest floor.

type of sprayer	amount applied	under shrubs	between shrubs
hand	12 l/ha	9(6-17)	2(1-6)
motor	8 l/ha	3(2-3)	2.5(1-6)

* 0.001 ml/dm^2 ~ 1 liter/ha.

Table 3. Percentage mortality of isopod, collembole and carabid after 10 days on a completely or partly treated soil substrate with 1.25% 2,4,5-T.

		control	2,4,5-T
Philoscia muscorum	completely	20	90
	partly	20	60
Onychiurus quadriocellatus	completely	0	94
	partly	1	17
Notiophilus biguttatus	completely	8	100
	partly	0	30

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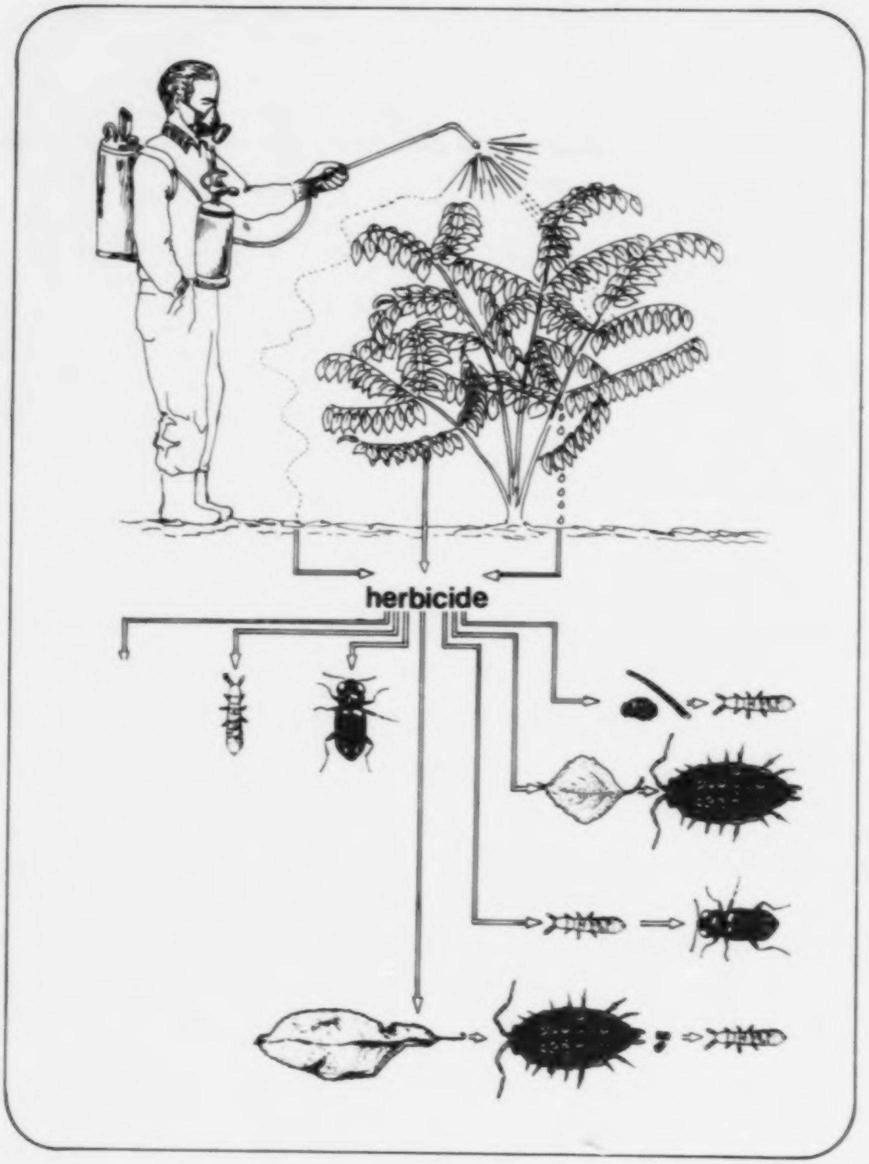


Figure 1: Possible ways of contact of soil fauna species with a herbicide after spraying.

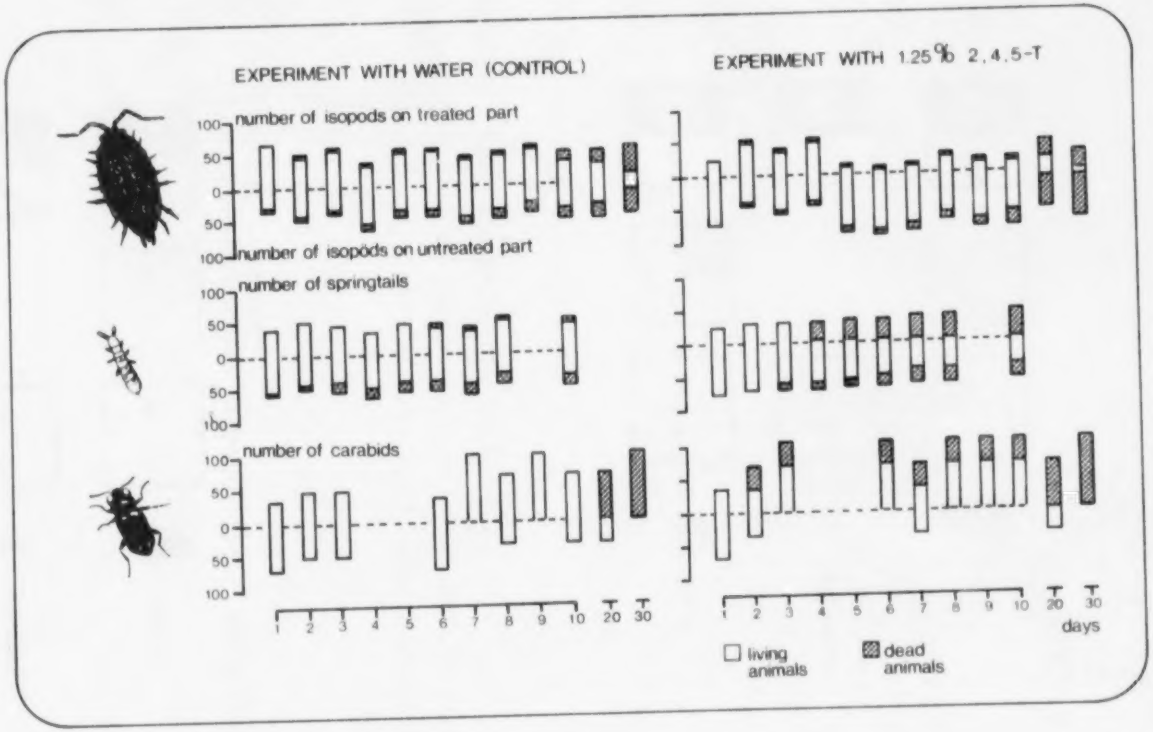


Figure 2: Distribution of first choice of 10 specimens entering a soil substrate partly (right half) sprayed with water (control) or with a low or high dose of 2,4,5-T ester.

Figure 3: Distribution of residence time in percentages of 10 specimens during 15 minutes on a soil substrate partly (right half) treated with water (control) or with a low or high dose of 2,4,5-T ester.

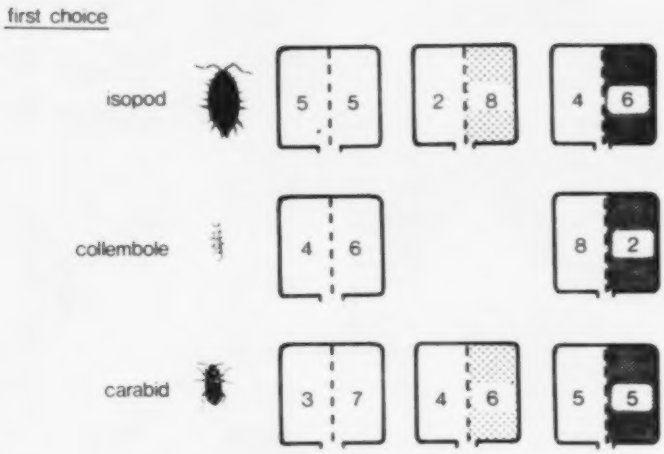
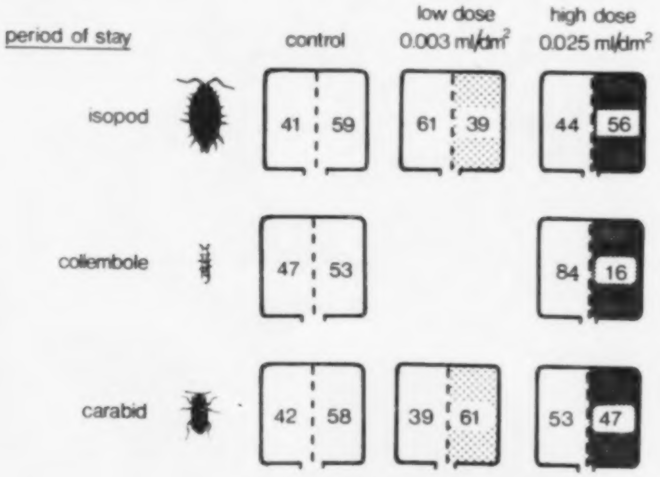

first choice
isopod
5
5
2
8
4
6
collembole
4
6
8
2
carabid
3
7
4
6
5
5

Figure 4: Distribution in percentages of living and dead (hatched) specimens of isopods, collemboles and carabids on soil substrates partly treated with water (control) or with a 1.25% solution of 2,4,5-T ester.


period of stay
control
low dose
0.003 ml/dm²
high dose
0.025 ml/dm²
isopod
41
59
61
39
44
56
collembole
47
53
84
16
carabid
42
58
39
61
53
47

Because of its low assimilation efficiency large amounts of litter have to be ingested. In this way considerable amounts of 2,4,5-T are ingested too. Predators like the carabid may ingest considerable amounts of 2,4,5-T due to bio-accumulation. The persistence of 2,4,5-T in cherry leaves and litter contained respectively 200-400 and 100 ppm 2,4,5-T. The various ways that soil fauna can ingest 2,4,5-T are: consumption of sprayed cherry leaves, contaminated litter items, and contaminated prey. The necrophagious behaviour of the springtails may result in consumption of died, contaminated relatives. Ingestion of 2,4,5-T may result in a changed rate of consumption and an increased mortality as well.

The effects of different treated food items on consumption rate and longevity of collembole, isopod and carabid are summarized in Table 4. When a number of litter components (birch litter, larch needles and green algae Pleurococcus) are offered to the springtail, the effects are quite different. With the algae the springtail shows a marked decrease of consumption, whereas mortality increases. The effects on mortality with birch litter and larch needles are smaller, with larch needles there is also a decreased consumption rate. The isopod also consumes less treated than untreated birch litter and shows an increased mortality. In contrast with the findings above, breakdown of cherry litter collected freshly every week is not hampering at all. Primary breakdown by the isopod as well as secondary breakdown of the litter fragments in the isopod pellets by growth of fungal hyphae and grazing of springtails, is better with treated than untreated cherry litter. Isopods show a significantly decreased mortality whereas the mortality of the collemboles is somewhat increased. Observations and some minor experiments about the effects of necrophagy with the springtail did not reveal that the ingestion of herbicide by consuming springtails killed by the herbicide does affect the collemboles adversely. Predation by the carabid of contaminated springtails causes a considerably increased mortality however. This has been observed with prey that was still mobile after being sprayed with a 0.3% solution of 2,4,5-T and with prey killed by 2,4,5-T. Mobile prey is strongly preferred to immobile prey, but when only the latter is present it is eaten eagerly.

Table 4. Effects of treatment of food with 2,4,5-T on consumption rate and mortality of isopod, collembole and carabid, expressed as percentage of increase (+) or decrease (-) relative to untreated food.

consumer	food type	consumption rate	mortality
collembole	birch litter	-22%	-12%
	larch needle	-50%	- 4%
	algae	-95%	+40%
	isopod pellets of cherry litter	+11%	+ 5%
isopod	birch litter	-36%	+15%
	cherry litter	+ 7%	-39%
carabid	springtails	-68%	+73%

Table 5. Percentage mortality of collembole and carabid after 10 days when sprayed with 0.3% 2,4,5-T or unsprayed, with or without addition of untreated food

	without food addition		with food addition	
	control	2,4,5-T	control	2,4,5-T
collembole	0	48	1	24
carabid	7	25	25	35

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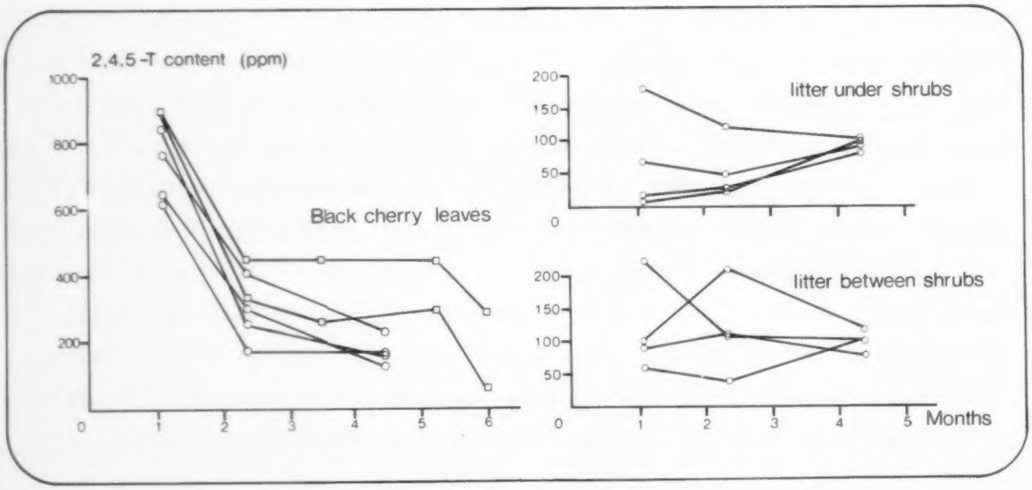

Figure 5: 2,4,5-T content (ppm) during a 6 months period of time of black cherry leaves and litter after spraying a 0.75% solution of 2,4,5-T ester.

The influence of feeding uncontaminated food upon the specimen's sensitivity was tested by comparing experiments in which after spraying unsprayed food was added to the experiments described in 2. From Table 5 it is clear that with addition of uncontaminated food the mortality of collemboles and carabids is reduced. This reduction is not caused by a lower mortality due to the absence of starvation, as in the control experiments in which no food was added, the mortality was very limited. Furthermore, an experiment with collemboles was designed in which in the centre of a moist soil substrate treated or untreated food was added. With untreated food the springtails strongly preferred the food area. After treatment of the food with 1.25% 2,4,5-T about 50% of the springtails avoided the food area initially, but on the third day the numbers of springtails in the food area were about equal to the numbers in the control experiments.

4. Impact of varying environmental conditions

The laboratory experiments described in the preceding sections were conducted at a fixed temperature (15°C), which is the mean litter temperature in our forests during and after the period of spraying operations. The relative humidity was kept at 90% and the soil moisture content was about 22%. However, under natural conditions these variables fluctuate locally and temporarily. Therefore, the effects of variable moisture and temperature levels were investigated in further detail.

In our direct observation experiments with a partly treated substrate (par. 2) the field moisture fluctuations were imitated by treating half of the moist substrate with a 2,4,5-T solution or with extra water. In the control experiment all three experimental species had a slight preference for the sprayed (wetter) part of the substrate (cf. Fig. 3). When the substrate is sprayed partly with the same amount of an aqueous solution of 2,4,5-T the preference is opposite; the repellent action of 2,4,5-T decreases the preference for a moist substrate. An experiment was also designed in which springtails were exposed to a dish with a moist centre sprayed with 2,4,5-T, surrounded by a dry sand substrate. During the experimental period of 17 days all the collemboles stayed on the dry substrate and about 25% of them died due to desiccation.

Soil temperature has a distinct diurnal rhythm. Therefore, an experiment was carried out in which collemboles were treated with 1.25% of 2,4,5-T and then placed in climate rooms with constant temperature of 15° and 25°C, or with a temperature fluctuating between 15°C (night) and 25°C (day). After 10 days the mortality percentage with a fluctuating temperature was about the same as with constantly 25°C; respectively 60 and 65%.

However, at 15°C the mortality percentage was 45%. So obviously in this experiment the limited periods of maximum temperature determined the effect of the herbicide, whereas the mean temperature gives an underestimation of the possible effect of the herbicide.

Concluding remarks

One of the main problems in evaluating pesticides effects in laboratory experiments is the discrepancy between laboratory conditions and the situation in the field. On the forest floor there is a patchy distribution of the herbicide. This might enable soil animals to avoid or withdraw from the treated areas. However, the places where 2,4,5-T drips on the forest floor very likely will be tied with the places where normally rain is dripping on the ground. The moisture content will be high at those places. These moisture patches provide optimal conditions for isopod and collembole, in respect to food and survival (Den Boer 1961; Verhoef 1978). Therefore, the presence of 2,4,5-T will be tied with the presence of food and moisture. Despite the repellent action of 2,4,5-T, over a longer period the chances of getting into contact with 2,4,5-T will therefore be high. Moreover, from these results it can be concluded that the classical LD 50 tests with a continuous exposure to the pesticide give an overestimation of the herbicide's effect. Nevertheless, in an experimental set-up which simulates the natural conditions to a greater extent, the herbicide is still toxic for isopod, collembole and carabid at equal amounts which occur in the forest floor.

It can be concluded from the experiments with contaminated and uncontaminated food that consumption of litter and prey contaminated with 2,4,5-T during and immediately after spraying may cause harmful effects on representative species of the soil fauna and consequently it is expected that fragmentation processes performed by these soil fauna species will become hampered. Treated cherry leaves which come available for consumption after leaf-fall do not cause harmful effects. Fragmentation of this litter is enhanced by spraying as well. The consumption of uncontaminated food however, might decrease the herbicide impact by direct contact, although mostly the chance of direct contact will be tied with the presence of contaminated food. Although it would be interesting to study these phenomena over a longer period of time, it is questionable whether this will be possible in laboratory experiments, because over a longer period there may occur significant aberrations in food consumption as Van der Drift (1975) found with the millipede *Glomeris marginata*.

Besides food, the temperature and moisture fluctations in the forest litter may influence the amount of effect.

From our results and observations it is concluded that variable or varying environmental conditions do not diminish the toxic effects of the herbicide. Fluctuating temperatures may reinforce the herbicide's effects, whereas the repellent action of the herbicide may retain soil animals on a dry area of the soil substrate and so increase the chance of fatal desiccation. A temperature increase will promote the mobility of the animals, and so the chances to get into contact with 2,4,5-T. Moreover a higher temperature will increase the animal's metabolism resulting into raised ingestion of 2,4,5-T, but also an increased breakdown.

Without being able to assess fully the effects of all these processes, it is clear that the irregular distribution of animals, food, moisture and pesticide on the forest floor as well as temperature fluctuations have to be incorporated in risk assessment procedures. However, in developing laboratory tests for risk assessment of pesticides and other contaminants with respect to the soil fauna, it is questionable to what extent it is worthwhile to complicate experiments in order to approach natural conditions as much as possible. Moreover, it is questionable whether it is of interest to predict exactly the amount of effect of the herbicide under mean constant conditions or to assess roughly the possible toxic effects under extreme conditions. From the experiments described above it has been made reasonable that in the testing programs these extreme conditions have to get more attention. This has to be accompanied by a thorough analysis of the niche parameters of the soil fauna species under study in order to get laboratory experiments which are suitable for assessment of toxic effects of pesticides on the soil fauna.

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EFFECTS OF DRAINAGE UPON THE SPIDER FAUNA (ARANEAE) OF THE GROUND LAYER ON MIRES

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INTRODUCTION

The proportion of peatlands, mires, has been high in northern Europe, but intensive human activity has changed the situation. In Finland, for example, about half of the peatland area has now been ditched, mainly for forestry but also for agriculture and peat industry. The mires, once typical and common habitats, are nowadays one of the ecosystems undergoing greatest changes in northern Europe.

In the present paper, the effect of drainage upon spiders on Sphagnum mires is discussed, and comments are offered on the usability of the spider fauna data for monitoring the situation of mire habitats.

STUDY AREAS, MATERIAL, AND METHODS

Bog Karevanrahka is situated near Turku, southwestern Finland, and bog Vissmosse near Hörby, southernmost Sweden. The study habitats at Karevanrahka were three natural sites with Sphagnum (an Alnus swamp, a Phragmites fen, a Calluna peat bog) and a peat harvesting area. This man-made site consisted of dry peat isthmuses without Sphagnum. The harvesting area was a Calluna peat bog before human activity. There were 10 pitfall traps in each site at Karevanrahka from April to September. At Vissmosse, the study included a natural Eriophorum-Calluna-Sphagnum bog and a dried part of the bog, now a Calluna-Cladonia site (without Sphagnum). There were 20 traps from May to October. The material consisted of 1207 identifiable spider specimens from Karevanrahka and 2146 from Vissmosse.

RESULTS AND DISCUSSION

At Karevanrahka, the number of species and individuals was highest in the Phragmites fen, but no clear difference was found between sites. The lowest Shannon index was observed in the man-made site, but differences in diversity were also small (Table 1). At Vissmosse, the species and individual numbers were higher in the dried site. This was probably due to the fact that both hygrophilous (real mire species) and xerophilous spiders occurred in the material. The diversity of spider fauna in the dried part of the bog was smaller than in the natural part (Table 2).

TABLE 1. Structure of spider fauna at Karevanrahka

	Alnus	*Phragmites*	*Calluna*	Harvesting area
Species number	38	48	36	37
Ind. number	226	355	338	388
Shannon index	2.76	2.98	2.85	2.57

TABLE 2. Structure of spider fauna at Vissmosse

	natural bog site	dried bog site
Species number	54	62
Ind. number	728	1418
Shannon index	3.11	2.80

The proportion of small soil (*Sphagnum*) dwelling spiders was decreasing after the drainage: e.g., 48% of individuals in the natural site were linyphids as against 21% in the dried site at Vissmosse. Xerophilous lycosids and gnaphosids became more dominant in the human-influenced sites: *Xerolycosa nemoralis* (Westring) 36% of individuals at Karevanrahka, and *Pardosa nigriceps* (Thorell) 23% and *Gnaphosa leporina* (L. Koch) 15% at Vissmosse. The diversity of spider faunas has sometimes been used as an indicator of the situation of habitats (Uetz, 1975). In the present material, no clear difference was found in diversity between natural and man-made sites. However, the man-made sites were rather old (10 to 15 years), and their fauna may thus have reached a stable situation. As the epigeic fauna (pitfall trap material) changes rapidly after environmental changes (Huhta, 1971), the diversity may be more useful indicator immediately after the habitat has changed.

There were typical abundant species in each site. At Karevanrahka these included *Pirata hygrophilus* Thorell, *Bathyphantes parvulus* (Westring), and *Wideria melanocephala* (O. P.-Cambridge) in the *Alnus* swamp; *Pirata insularis* Emerton and *Maro lepidus* Casemir in the *Phragmites* fen; *Pardosa hyperborea* (Thorell) and *Scotina palliardi* (L. Koch) in the *Calluna* peat bog; and *Xerolycosa nemoralis* and *Pardosa lugubris* (Walckenaer) in the harvesting area. At Vissmosse, typical species in the natural site included *Pirata uliginosus* (Thorell), *Lepthyphantes ericaeus* (Blackwall), and *L. cristatus* (Menge), and in the dried bog site *Gnaphosa leporina* and *Meioneta affinis* (Kulczynski).

Certain dominant species could perhaps be used for monitoring the situation of mire habitats (Koponen, 1979). Such indicator species of a site could be Pirata hygrophilus, P. insularis, Pardosa hyperborea and Xerolycosa nemoralis at Karevanrahka, and Pirata uliginosus and Gnaphosa leporina at Vissmosse (Tables 3-4).

TABLE 3. Rank order of certain abundant species at Karevanrahka

	rank in			
	Alnus	Phragmites	Calluna	Harvesting area
Pirata hygrophilus	1	-	-	-
Bathyphantes parvulus	2	45	31	13
Wideria melanocephala	9	-	-	-
Maro lepidus	21	5	-	-
Pirata insularis	-	6	-	-
Pardosa hyperborea	-	8	1	26
Scotina palliardi	-	28	7	-
Xerolycosa nemoralis	-	-	-	1
Pardosa lugubris	18	-	-	2

TABLE 4. Rank order of certain abundant species at Vissmosse

	rank in	
	natural bog site	dried bog site
Pirata uliginosus	1	10
Lepthyphantes ericaeus	4	40
L. cristatus	7	-
Gnaphosa leporina	-	2
Meioneta affinis	-	8

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STUDIES ON REQUIREMENTS AND POSSIBILITIES OF ZOO-AMELIORATION OF AFFORESTED ARABLE LAND

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Results of the first stage of our investigations, presented at the Sixth International Soil Zoology Colloquium in Uppsala (Szujecki 1977), defined the requirements of forest soil macrofaunal reestablished on afforested arable land. The search for the right directions of soil fauna reestablishment on afforested arable land was preceded by studies of biological characteristics of afforested arable soils; in comparison with forest soils, afforested arable land, it was found, inhibited the development and the functioning of the reestablished forest ecosystems. These bio-indicative features included the following:

1. Concentration of macrofauna and its activity in surface soil layers
2. High mobility of epigeic fauna
3. Occurrence of xerothermophile forms
4. Too small proportion of saprophages in soil fauna, as compared with phytophages and predators
5. Low average biomass of the specimens and low level of biomass of total macrofauna
6. High average biomass of specimens in populations of epigeic species (this is characteristic of poor habitats and pioneering succession stages)
7. High proportion of the spring type Carabidae species of short life cycle and high maintenance cost
8. Changes in sexual index of Carabidae population characteristic of poor habitats.

The enumerated characteristic features of macrofauna are responsible for the limitation of the circulation of elements (especially organic carbon and nitrogen) into the litter layer, for the acceleration of circulation, and for significant losses of energy connected with higher maintenance cost of soil macrofauna on afforested land. Analyses of soils, especially analysis of fractionated humus parts confirmed these findings, thus substantiating the thesis of different circulations of elements on afforested arable and on forest land.

The purpose of zooamelioration measures would be to reestablish the forest soil fauna. Such re-establishment would control the circulation of biogenes, it would effect penetration of the circulation into the deeper layers of soil and reduction of faunal maintenance cost, intensification of humifying processes, and acceleration of succession processes. Saprophages were assigned the major role in zooamelioration procedures. They essentially affect humus formation and improvement of physical properties of soil and are deficient in young cultures and stands on afforested arable soils. It did not seem rational to introduce the organisms of higher trophic levels of zoocenoses into the existing systems. These animals would have insured the transfer of matter in ecosystems of afforested land without providing a nutritional basis. It was, therefore, assumed justified to accept, as a principle of zooamelioration measures, some preliminary phytoamelioration treatment, e.g. introduction of Washington Lupine, wildblackberry, spruce undergrowth, or introduction of some organic bulk of slow decomposition rate, such as fragmented pine bark or sawdust. These measures were designed to facilitate the introduction of some species of saprophage animals into afforested arable land, e.g. _Nopoiulus_ _fuscus_ Am. Stein, Diplopoda, or to ensure protection of local saprophages.

A possibility of reducing the impact of predators on soil saprophages was also examined; this was assumed to be achieved through a change of the compounds of exploiting or competitive character that occur in various layers of forest floor, both litter and mineral soil. Artificial colonization of _Formica_ predator species was to serve the purpose. In order to accumulate more knowledge on the possibilities of controlling the changes occurring in soil macrofauna concentrations, the effect of various kinds of soil preparation to afforestation was studied. By distributing the designed phytoamelioration procedures within growth lines of forest stands on afforested arable land diverse effects were obtained which changed the present-day systems in communities of soil macrofauna.

Arable soil may be prepared for afforestation by employing various kinds of cultivation. Among the various ways of ploughing, e.g. striped, shallow total, and deep total, the latter produces the greatest changes in macrofauna. The negative effect of deep ploughing upon reestablishment processes of communities of forest macrofauna manifests itself through preference for xerothermophile, eurytope, and hemizoophage forms, through an increase of the degree of synanthrophization in this habitat, and it also leads to retardation of the succession process. Thus, striped ploughing seems to be most recommendable.

The introduction, at the same time, of bark, and especially of pine sawdust causes a reduction of macrofauna occurrence already after two years; it is only Chilopoda and Lumbricidae that show increased density which is the highest in areas fertilized with bark in the amount 270 m^3/ha. The use of a mixture of 180 m^3 bark and 90 m^3 sawdust per 1 ha reduces the density of macrofauna to 60%, compared with the control plot. The application of sawdust at only 180 m^3/ha reduces macrofauna to 35%. A quantitatively significant decrease occurs among phytophages, as their density in relation to growth inhibition of weeds is five times lower than that on non-fertilized plots.

Both surface phytophages and eudaphic Selatosomus larvae (characteristic of fallow and first successional stages of afforested land) suffer this limitation. Also Carabidae undergo limitation, whereas the population of Staphylinidae is significant. On areas fertilized only with bark the density of saprophagic Diptera larvae undergoes reduction. Thus, phytophages which depend upon an optimal nutritional basis, and mobile species of zoophages respond most readily to the treatment of bark and bark with sawdust. The introduced organic matter exerts influence on local saprophages in a variety of ways, but it certainly allows the introduction of species not occurring in young afforested areas, e.g. Nopoiulus fuscus - a species characteristic of the youngest pine stands in Poland. As a saprophage and a micophage it has a fairly wide trophic spectrum whose component is also pine bark in various degrees of decomposition. Discharged excrements of this creature (in young forests, on average 16.6 kg/ha dry matter annually) contain organic matter and are deposited in various parts of soil profile, thus enriching the soil with easily decomposable compounds. In addition, they become a place of vital activity of microorganisms.

A limitation of the degree of mechanical cultivation of soil and the introduction of fragmented pine bark with an addition of sawdust creates a possibility that inhibits mineralization processes characteristic of afforested arable land. This procedure seems to be advantageous, since nutritional requirements of young pine forests is not high at this stage. Conditions are created for the development of saprophagic fauna favourable for humification processes typical of forest soils. Development of this fauna is favoured, for example, by preceding the treatment described above with a crop of Washington Lupine on arable soils designed for afforestation. The introduction of wild blackberry into afforested pine stands (which should be done, optimally, between 10-40 years of age of a forest stand) increases the density and biomass of macrofauna, especially of facultative saprophages and soil zoophages, and limits mobility of the latter. Moreover, this kind of treatment raises the level of macrofauna in deeper layers of soil (depth 10-20 cm) which supposedly may cause the deeper distribution of organic carbon and nitrogen in soil profile, as well as circulation of these elements between litter and mineral soil.

The introduction of deciduous undergrowth creates great possibilities of influencing soil of pure pine forest stands. However, this kind of treatment is practically impossible when the population of fallow-deer is high. Hence, in some afforested lands of North-West Poland, pine is introduced together with common spruce which produces forest stands with rich undergrowth. In 45-year old forest stands spruce undergrowth exerted a limiting influence on the whole macrofauna and showed preference for species characteristic of earlier succession stages of macrofauna. The spruce undergrowth is not recommended as the one favouring restitution processes of forest fauna.

The last procedure of zooamelioration possible in all age groups of afforested arable land is an artificial introduction of Formica ants. The influence of ants upon other soil fauna depends on the ants species and the species of prey animals. First of all, it was observed that increase of macrofauna density depends on distance of its occurrence from ants nests. The litter-soil macrofauna is the most limited by Formica polyctena, and to a smaller degree by Formica rufa. Impact of F. pratensis is more differentiated spatially and thus more difficult to define. It is mainly directed to small phytophages and to small litter zoophages, whereas F. polyctena mainly limits saprophages and F. rufa a different food group the zoophages. The dominant species of macrofauna are the most strongly limited. Furthermore, it was observed that small ants (Tetramorium, Myrmica) are more numerous in the neighbourhood of ant-nests of Formica species in the soil layer, whereas on the surface of the forest floor mobility of these insects increases with the distance from Formica ant-nests.

Results of investigations on justification of using the larger ants to control trophic levels in communities of soil macrofauna do not indicate that representatives of Formica species would influence an increase of population density of big saprophages in litter or mineral soil by limiting the population of epigeic predators, such as Carabidae. Within the area of the ants' influence their impact on macrofauna is of a total character. Soil saprophages are also subject to their influence; at adult stage they become victims of species of Formica genus. It may be assumed that in the presence of ants there occurs a change of one group of non-specialized predators into another. In addition to what has been said above, the range of ants, even those artificially colonized, is too small in relation to the area of a forest stand to expect that their presence would radically change biological activity in the Ap accumulation horizon.

However, the knowledge of structure and function of forest biocenoses is too scanty to state that the discussed studies of trophic and competition interrelationship of soil and epigeic macrofauna have exhausted all the possibilities of ants use for zooamelioration purposes. On account of specific differentiation of Formica species, the distribution of various taxa of macrofauna seems to indicate that the presence of this group of insects favourably affects multiplication of directions of dry matter transfer in poorly differentiated habitats such as newly afforested lands. The complexity of the matter circulation may, in turn, exert a stabilizing influence on the functioning of these ecological systems.

It can be concluded that, although the processes of macrofauna communities restablishment and shaping of spatial and time structures of its numerous functional groups are long-term processes, there seem to exist high possibilities of their controlling and accelerating adequate technical procedures, including zooamelioration ones. The purpose of such activity would be to create conditions for correct circulation of biogenes in the environment of afforested arable land throughout the whole life cycle of new forest. An additional aspect of the phyto- and zooamelioration measures discussed above are the enrichment and activation of microorganisms, including the species antagonism to root polypores and creating the conditions for the occurrence of numerous valuable compounds of forest entomocenosis connected with wild blackberry. The production of ecological systems similar to those in forest sites would mark a significant progress on the way to reestablishment of natural habitats on afforested arable land; this would not, however, solve the ecological problems which accompany total clearing of pine stands.

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EFFECTS OF FIRE ON SOIL FAUNA IN NORTH AMERICA

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INTRODUCTION

In forest soils the vast majority of the invertebrates live in the surface organic layers, or forest floor. This floor, consisting primarily of leafy material from the trees, is divided into three layers. From the surface down these are: the L (litter) layer - recently fallen material still intact; the F (fermentation) layer - broken and partially decomposed material; and the H (humus) layer - material so far decomposed that its origin is not evident. Of these layers, the L, which is loose in structure and thus usually quite dry, affords the most inhospitable environment in the floor for invertebrates and few are found there. The lower layers, toward the mineral soil, are more compact and moist, and many animals are found in these F and H layers, especially the latter which lies directly above the mineral soil. In the mineral soil the density of animals decreases with depth from the surface. The vertical distribution of mites and collembolans can be illustrated from data collected in a loblolly pine (Pinus taeda L.) forest in the Southeastern United States (Metz and Farrier, 1973). The percentages of these animals in the L, F, and H organic layers and the 0-1, 1-2, and 2-3 cm of mineral soil were 2, 34, 48, 9, 4, and 3, respectively.

The forest floor is involved in all forest fires and in fact practically all fires begin in this part of the forest. There are two general types of forest fires. Wild fires are caused by man, unintentionally or maliciously, and by lightning. Prescribed fires are those set by man to achieve a certain purpose - create a seedbed for a new generation of trees, kill young trees of certain species which are not wanted in the forest, or to reduce the fuel so that if a wild fire occurs there will be less biomass in the forest to burn and thus damage will be kept to a minimum. Since prescribed fires are carefully controlled by man they are often called controlled fires. The control consists of having fire lanes around the area to be burned, burning when the wind and humidity are just right, and when the moisture content of the floor is such that only part of it will burn. Since fire is a relatively economical procedure for achieving certain desired objectives in the forest it is being used more and more in the USA. Of course, if standards for air and water quality cannot be met, its use may decrease in the future.

Any fire in the forest is going to kill some soil invertebrates. The extent of damage is related directly to the amount of heat generated. In addition to killing animals directly and indirectly, fire changes the community structure. A fire severe enough to consume most of the forest floor can produce a food shortage for carnivorous as well as phytophagous animals.

Wildfires often occur when the forest floor is dry. Under these conditions the floor is completely reduced to ashes and all the invertebrates in the floor, except those that fly away, are killed. Since much heat is generated under such conditions, many of the animals in the surface layers of the mineral soil are also killed.

A well executed fire consumes only the surface layer of needles and leaves; that is, the L and part of the F layer. Since most invertebrates inhabit deeper, wetter layers, relatively few are killed.

Effects of fire on the forest ecosystem have been studied for many years, but most effort has been concerned with the vegetation, primarily trees. Although work on fire and the soil fauna has been in progress for some time, there is still a paucity of research results.

REVIEW OF SPECIFIC RESEARCH

Some work has been done with various insects that spend but a part of their life cycle in the forest floor or mineral soil.

Fires in Australia, both prescribed and wild, reduce the populations of stick insects (phasmatids) to a very low level if the forest floor is completely consumed. Both nymphal and adult stages are affected, and the burning has a long term depressing effect on populations (Campbell, 1961). Beetle populations in an area of shrub steppe vegetation in southeastern Washington that had been burned by a wildfire were examined and compared with the populations of an unburned area. Of the four species studied, all were found in both areas, but the populations of two species were significantly reduced by burning (Rickard, 1970).

The effect of buring 0.4 ha (1-acre) plots on the invertebrate component of grassland in Ohio was brief, and populations were back to normal in 3 months. Sampling was done by the vacuum method, and so few soil fauna species were involved (Bulan and Barrett, 1971). In a study of this type, small plots and the mobility of the insects sampled could have masked the effects of the burning. Beetle populations in Florida pine forests that had been burned annually were compared to those in grass that had not been burned for 10 or more years. Of the total number of carabids trapped, 85 percent were taken in the unburned plots (Harris and Whitcomb, 1974). In New Jersey, the distribution of the periodical cicadas (_Magicicada_ spp.) was studied in 1902 and in 1970. In the 1970 study, the insects had disappeared from many of the locations where they were found earlier. Disappearance was attributed to destruction of forests, forest fires, and urbanization (Schmitt, 1974).

Prescribed fire can be used as a sanitation measure in the forest (Miller, 1978). The red pine cone beetle (*Conaphthorus resinosue* Hopkins) destroys the cones of red pine (*Pinus resinosa* Ait.) and greatly reduces seed production. The adults of the beetles spend the winter months in the forest floor and burning during this period greatly reduced or eliminated the damage caused by the insect. In Michigan the maple leaf cutter (*Paraclemensia acerifoliella* (Fitch)) reduces the leaf area of sugar maple (*Acer saccharum* Marsh) and thus causes a decrease in flow of the sap used in maple syrup production. Prescribed fire kills the pupae while they are in the forest floor. Pupal mortality was nearly 90 percent and was higher than chemical control percentage obtained by other workers using Carbaryl (Simons et al., 1977).

For what might be called the "true soil fauna", that is, those animals which spend nearly all of their lives in the organic or mineral soil layers, practically all studies show the animals are decreased in number by fire. These findings are world wide as evidenced by work in many countries outside the USA.

In Austria, mites, the most common soil organisms collected, were less abundant in burned areas (Jahn and Schimitschek, 1950). In the coniferous forest of northern Sweden more mites were found in unburned than burned forest floor, but the author ascribed the difference to normal variation in their population (Forsslund, 1951).

In Finland, clearcutting forests that had a thick raw humus layer and then burning the areas a year later greatly reduced the population of oribatid mites. Five years after the burn the oribatids still showed no sign of recovery (Karppinen, 1975; Huhta et al., 1967, 1969). After wildfires swept through *Pinus radiata* plantations in Australia, the soil fauna were examined on sites that had been lightly and severely burned. The populations in the severely burned areas were lower than in lightly burned areas (French and Keirle, 1969). In Canada, the density of soil fauna was found to be decreased in both the forest floor and surface 5 in. of mineral soil 2 years after a slash burn (Vlug and Borden, 1973). "Fuel reduction fires" of even low intensity in Australian dry forests caused substantial mortality of soil fauna in both the forest floor and surface soil. On these sites it was estimated that it would take from 2 to 6 years for the fauna populations to return to a prefire level (Leonard, 1977).

A prescribed fire in western Australia (Bornemissza, 1969) eliminated all organisms from the forest floor and 85 percent in the upper 5 cm of mineral soil. Two or three years after the fire the insect fauna recovered fully, but mites, especially oribatids, required 4 or 5 years for populations to return to normal. The influence of prescribed burning on soil fauna under two species of *Eucalyptus* was studied in Australia (Springett, 1976). The unburned plots had 6 times the number of animals per unit area, and 1.5 times the number of species, when compared to the burned plots. Only large animals such as spiders, pill bugs, and millipedes, which could be identified without magnification were tabulated. The author also states that a decrease in the number of species and population density was still evident at the end of the prescribed burning rotation, presumably 5 to 7 years, but presents no data on the subject. In burned and unburned Australian eucalypt forests, ant fauna were intensively studied (Majer, 1978). Animals were collected in pitfall traps. Even though more ants were collected on the unburned than on the burned plots Majer found that both areas were "characterized by a high ant species richness and moderate ant equitability".

Earliest work in the USA on effects of fire on soil fauna was done in the longleaf pine (Pinus palustris Mill.) region of the South (Heyward and Tissot, 1936). Stands that had been protected from fire for at least 10 years were compared with stands on similar soils that had been burned frequently. In this study, the larger animals were sorted by hand and the smaller ones were extracted with funnels. Although no statistical tests were made it was obvious, from the large differences found, that fire depletes the fauna.

An indirect estimate was made of the larger fauna by counting holes at least 1.27 cm (1/2 in.) in diameter on numerous spots on each study. This was done clearing away all organic material and exposing the mineral soil. In general about 10 times as many holes were noted on the nonburned plots as on the burned ones, and these holes were attributed to beetles and small mammals. Holes smaller than 1/2 in. were ignored because many were disturbed when the organic layers were removed and it was felt the count would be inaccurate. Five times as many animals ranging in size from mites to millipedes were found in the organic layer on the nonburned plots and 11 times as many in the surface 5.08 cm (2 in.) of mineral soil as on the burned plots. Of the animals counted, about 85 percent were mites or collembolans.

From 1937 through 1941, a stand of loblolly pine in North Carolina was burned each year, and an adjacent stand of trees, not burned, was used as a control (Pearse, 1943). Area samples covering 3.25 sq. m. (36 sq. ft) were taken, and the material was sorted by hand and identified with no magnification. The control plot contained about 3 times as many animals as the burned one. In both plots, ants made up over half of the animals collected.

Prairie fires in Illinois reduced the populations of both soil fauna and surface insects (Rice, 1932). As in some other studies, ants were often found in greater numbers on burned than on unburned areas.

About a year after a major fire swept through the Pine Barrens of New Jersey, burned and nonburned sites were sampled for soil fauna (Buffington, 1967). Animals were separated from the substrate in liquid and no magnification was used - hence mites, collembolans and similar sized animals were not counted. Buffington found that both numbers of taxa and numbers of individuals were significantly less in the burned over area. Our further evaluation of his data shows that fire usually caused reductions in the indices of community structures of macroarthropods of the Pine Barrens (Table I).

TABLE 1. Detail of community structure* of macroarthropods from the New Jersey Pine Barren, burned and unburned sites (Calculated from data of Buffington 1967)

	H' Species Diversity ($\log_e$)	r_{ma} Species Richness ($\log_e$)	J' Species Equitability
Total macroarthropods			
Unburned	2.3730	6.1865	.6309
Burned	2.0464	4.4428	.6209
Ants			
Unburned	2.0429	1.9352	.7741
Burned	1.8593	2.5813	.6702
Spiders			
Unburned	2.0885	2.8237	.9509
Burned	.6932	1.4427	1.0000

*H' (after Shannon and Weaver, 1963), r_{ma} (after Margalef, 1958), J' (after Pielou, 1969)

Species diversity, richness and equitability (with one exception) were all lower in burned areas. Most of the change in diversity was caused by reduction of the richness component; equitability, as the other component of diversity, was affected very little by fire. Ants appeared to be least severely affected, with 2 species, *Formica fusca* L. and *Leptothorax pergandei* Emery, appearing more abundant in the burned than in the unburned areas. About 95 percent of the organisms collected were ants.

The community structure of soil microarthropods (e.g., mites and collembolans) from the New Jersey Pine Barrens also reflected the effects of fire frequency of the sites they inhabit (Dindal, 1979). Six vegetative sites with various histories of burning were sampled and three indicies of the community structure of microarthropods were determined (Figure 1). Group diversity was highest in the pitch pine lowlands and

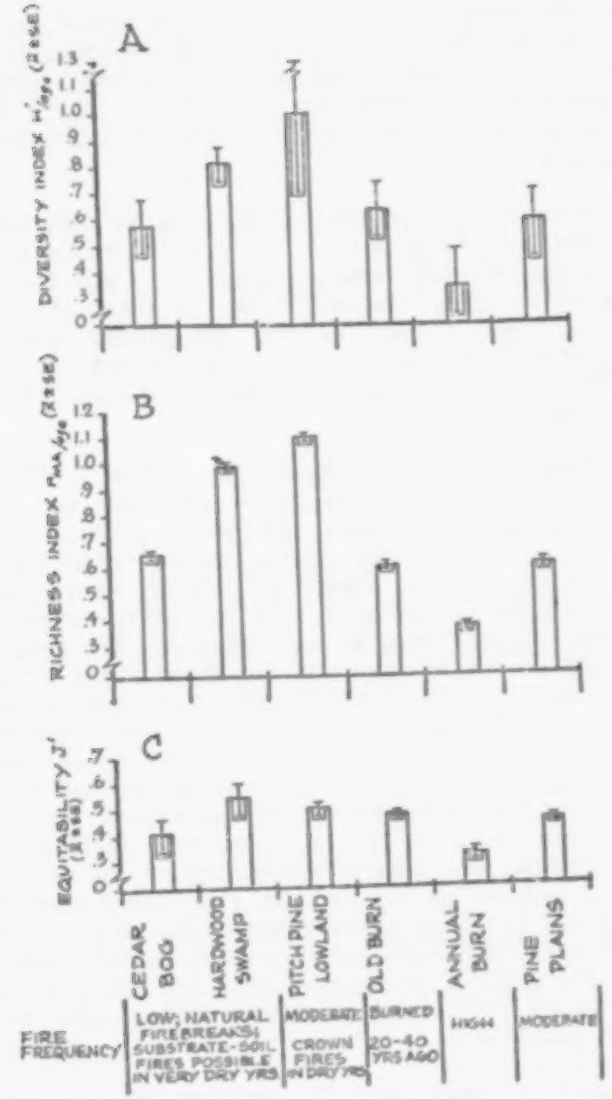

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Figure 1. Indicies of community structure of soil microarthropods of the New Jersey Pine Barrens: A) Group (order-suborder) Diversity, B) Group Richness, C) Group Equitability

the hardwood swamps which have the lowest frequency of ground-soil substrate fire (Figure 1A). Also in agreement with earlier findings of Metz and Dindal (1975), diversity was least in sites burned annually. Considering Figure 1B and C, group richness, in general, appeared to be the most important component determing the relative diversity levels. With the exception of annual burn sites, group equitability remained a rather constant diversity component, changing very little from site to site.

That the effect of fire is often transitory on soil fauna populations is evident from work in northern Idaho (Fellin and Kennedy, 1972). They sampled prescribed burns 1, 2, and 3 years old and found that 2 yr and 3 yr old burns had 2.3 and 7.7 times, respectively, as many animals as the 1 yr old burns. Most of the animals recovered were Coleoptera.

The influence of prescribed burning on nematode populations was studied in the pine forests of Louisiana (Harrison and Murad, 1972). One plot had been burned annually since 1915 and the control had not been burned since 1912. It was found that the total nematode populations differed significantly between the plots. The unburned one yielded significantly greater numbers of larvae and total populations in 17 of the 24 mos they sampled. No significant difference between plots was noted for adults.

Mesofauna were studied in loblolly pine in the Southeastern Coastal Plain of the United States on unburned, annually burned, and periodically burned plots (Metz and Farrier, 1973). The latter are burned every 4 or 5 yrs which is the general practice for prescribed burning in the South. The number of animals recovered from the unburned and periodic burned areas did not differ significantly but they both had significantly more animals than did the annually burned areas. Since the periodic plots were sampled about 4 yrs after being burned this period indicates the time it takes for them to recover. Of the animals collected in the above study 83 percent were mites and 11 percent were collembolans. Since taxonomy work on collembolans is further along than mite taxonomy it was decided to further analyze the results of the above for the collembolans at the species level (Metz and Dindal, 1975; Dindal and Metz, 1978). We found that burning, both annual and periodic, increases the species diversity of the collembolans in the F-H, the 0-1, and 1-2 cm layers. We also found that the general _Lepidocyrtus_ and _Tullbergia_ are represented on all sites and are generally associated with each other or with burned site conditions. Perhaps the differences in species that are found in these two genera are indicative of similar niches being filled under slightly different microhabitat conditions.

Not only are individual Collembolan species sensitive or tolerant to the action of fire, but also interspecific associations exhibit like sensitivities and tolerances. Comparing responses from the control to the most stressed site, there are reductions in the frequency of negative interspecific associations ranging from 36 percent to 0. Although the numerical complexity and number of associations are reduced by periodic burning some semblance of order within the community is retained. However, major reductions, as seen on annual burn sites, could have dramatic effects on negative feedback loops and community stability. Therefore, it appears that fire can cause shifts for and against certain species and associations of Collembola, thus modifying their total community structures (Dindal and Metz, 1977).

Apparently, moderate use of fire, such as prescribed burning every 4 or 5 yrs, does not permanently damage the soil fauna. The great recuperative powers of these animals seem to overcome such temporary setbacks.

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EXPERIMENTAL STUDY OF THE DIRECT EFFECT OF LITTER BURNING ON SOIL MICROARTHROPODS IN A DECIDUOUS TEMPERATE FOREST

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We have used an improved dry funnel extractor to carry out an experimental study of the direct effect of litter burning on soil microarthropods which are made up of mites and springtails. The material is the same one as compared to the automatic extractor used in the dynamic study of microarthropod behaviour towards soil water evaporation (VANNIER, 1970). The principle of the model resides in measurement of water loss, using a recording balance, conducted with rectangular slabs of soil covered with original intact litter layer and placed into a sieve, and in periodic collection of animals by an automatic fraction collector (Fig. 1).

Two kinds of analysis were undertaken at the same time :

1 - Temperature distribution at three levels in the soil sample (litter, soil surface, and 2-5 cm deep), and mass transfer evolution made up of water evaporation by natural convection and loss of matter due to combustion.

2 - Analysis of the animal fall out in successive collecting vessels at two hours intervals.

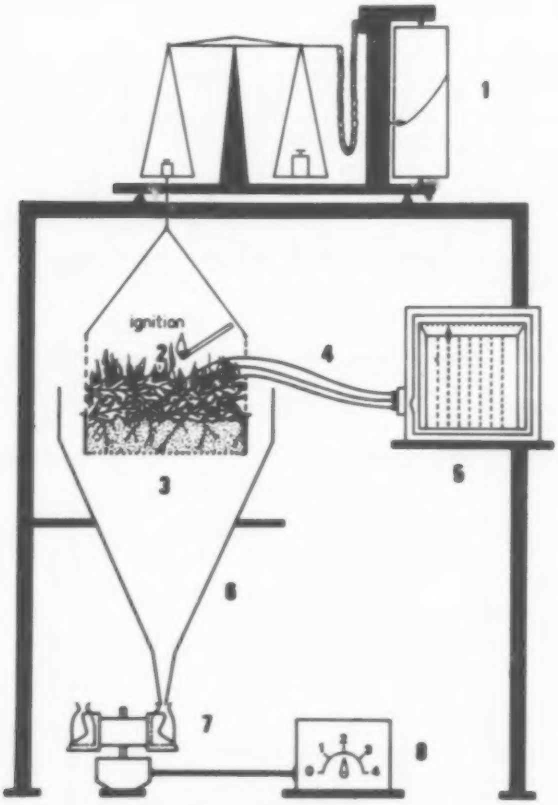
Twin soil samples (20 x 10 x 2.5 cm) were taken from Oak forest, one to be used as control, the other for litter burning experiment. Air conditions around the samples were maintained at 20°C and 70% R.H. Extraction took 13.5 days.

Ignition occured after four hours of extraction. The heat of the burning litter rose the temperature about 480°C no longer than about ten seconds, but at the soil surface and at 2.5 cm deep there was a very little rise in temperature for a short while, respectively from 16°C to 45°C, and from 15°C to 20°C. It followed that animals were not a great deal disturbed in the burned sample.

Epigeous forms like Sminthuridae and Entomobryidae Collembolans have shown a little increase in their activity,

Figure 1. - Schematic diagram of material for analysing the direct effect of litter burning on soil microarthropods.

(1. - Beam scales recording continuously the weight of soil sample ; 2. - Oak litter ; 3. - Sieve containing a rectangular slab of soil (20 x 10 x 2.5 cm) covered with original intact litter layer (mesh 2 mm) ; 4. - Probes measuring temperature distribution : litter, soil surface and 2.5 cm deep ; 5. - Recorder ; 6. - Funnel with steep sides ; 7. - Automatic fraction collector recovering microarthropods fall out at two hours intervals ; 8. - Timer.)



but endogeous forms like Isotomidae, Poduromorpha Collembolans and Oribatid mites were less affected by the prescribed burning. Thirty minutes after ignition, 15% of Sminthuridae left the soil sample, and 10% of Entomobryidae, compared to only 1.5% of Mesostigmata, 1.1% of Oribatei and 0.9% of Isotomidae.

Two hours later after ignition, the motor activity of all soil animals, expressed in terms of probability for an individual leaving the sample, rapidly diminished to attain low values in each group, as long as the moisture was available within the soil. When soil moisture content decreased beyond 24% (pF 4.2 permanent wilting point) for Collembolans and 16% (pF 5) for Oribatid mites, motor activity increased abruptly until fall-out was completed after 300 hours when extraction ended (see concept of water accessibility for soil microarthropods in VANNIER, 1970).

However no significant differences existed between two soil samples, one used as control, the other subjected to litter burning, in terms of the number of individuals in each zoological group (table 1). Due to heterogenous distribution of animals within soil, there were more individuals in the treated sample than in the control, except for Mesostigmata and Sminthuridae, as it is shown in the following table :

SOIL MICROARTHROPODS	COUNT IN CONTROL SAMPLE	COUNT IN BURNED SAMPLE
ORIBATEI	1,061	1,254
MESOSTIGMATA	854	706
NEELIPLEONA	9	13
SMINTHURIDAE	66	45
PODUROMORPHA	12	24
ISOTOMIDAE	309	315
ENTOMOBRYIDAE	213	268
Total	2,524	2,625

When considering population structure of a litter-dwelling species as Sminthurinus signatus (Collembola, Sminthuridae), it was possible to show the actual damage caused by the litter fire. The first-instar juveniles that hatched from eggs and sexually mature females were drastically affected, whereas the litter-fire halved their numbers. Reversely the number of other instars (2^d and 3^d instar juveniles, sub-adult males and females, mature males) did not differ significantly.

For further informations on related subjects, see VANNIER, G. (1970). - Réactions des microarthropodes du sol aux variations de l'état hydrique du sol. Techniques relatives à l'extraction des arthropodes du sol. Editions du CNRS, Paris, série PBI-RCP 40, 320 pages. and VANNIER, G. (1978). - Etude expérimentale de l'effet immédiat du feu de litière sur les microarthropodes d'un sol forestier. Bull. Mus. natn. Hist. nat., Paris, 3^e série, N° 519, sept-oct., 42 : 51-63.

SESSION VII: HUMAN IMPACT ON TROPICAL SOIL ECOLOGY

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EFFECT OF THE ANNUAL BURNINGS ON TESTACEA OF TWO KINDS OF SAVANNAH IN IVORY COAST

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The Tropical Ecology Station at Lamto (Ivory Coast) has been the center of integrated studies on all the local ecosystem types. The analytical approach has been an energetic evaluation of primary production and animal consumption (LAMOTTE, 1977) within the framework of the I.B.P.

The effect of the fire on the Thecamoebian fauna has been analysed in other countries : Metropolitan France and French Guiana (COUTEAUX, 1976a, 1977 and 1979 ; BETSCH *and al.*, 1979) in case of accidental, punctual burnings in the time and followed by more or less long spell during what the biotop tries to find again its stability.

The characteristics of the burnt savannas of Lamto consists in the fact that the burning is voluntary provoked each years, at the end of January, that is in the midst the dry season and that the populations have only one year of respite before the next perturbation.

A quantitive study of Testacea of two savanna ecosystems at Lamto was made on samples taken in April 1974.

I - DESCRIPTION OF THE BIOTOPS

Two sampling plots were located in a savanna, called "Savane du Rocher" which has few trees (Borassus aethiopum) and lies on tropical ferruginous soil. The microbiological activity of these soils is low (POCHON and BACVAROV, 1973 ; RAMBELLI *and al.*, 1973).

The sampling areas are located on : a transect extending from table-land savanna to the forest. The herbaceous covering of the upland savanna is dominated by *Hyparrhenia chrysargirea*, *H. diplandra* and *Andropogon schirensis*. The transect continues through a second savanna type down the slope with *Loudetia simplex* on a hydromorphic soil with pseudogley. Here the hydrous system is particularly evident since, in the dry season, a single heavy shower is sufficient to inundate it. In the rainy season the water-table is on the ground surface. The transect ends with a gallery-forest which extends along the marigot.

The annual burning gives a characteristic appearence to the savanna. The herbous covering consists of well defined grass tussocks of which, after fire, only burnt stalks remain. Between the tussocks there is bare earth where, at the beginning of the rainy season, the surface of the soil is eroded on the table-land and on the slope. When the sampling carried out, three months after the fire, the tussocks of Hyparrhenia and Loudetia were green but the roots were a little bared and burnt trails were still very evident.

II - TECHNIQUE

In each station, ten core samples were taken with a borer of 660 mm^2. At the distributional scale of the Protozoa such an area of soil surface is liable to contain several communities. In the savanna, one half of the samples were bored in the tussocks and the other in the bare soil. The cores were divided into two horizontal layers 1,5 cm thick. In the tussocks, the level upperlayer a consisted of the surface litter and stem bases and the level b was bored in the root mat.

The animal population density of the surface layer can be estimated by the technique of suspension-dilution of a fixed stained sample (COUTEAUX, 1975).

The biomasse can be calculated with respect to the volume of the living cells (COUTEAUX, 1976b, 1978).

Diversity was calculated using Margalef's Index.

III - RESULTS

A - Total density of the populations

The two principle characteristics of this protozoan fauna is their low numerical abundance as well as the number of species in the community. Mean population densities were : 2,46 living individuals per mm^2 representing 17 species in the savanna at Hyparrhenia ; 2,38 per mm^2 and 18 species in the savanna at Loudetia.

B - Influence of the depth (Table I)

		a	b	a + b
Savanna at Hyparrhenia	Bare soil	0,92	0,79	1,71
	Tussocks	1,52	1,70	3,22
Savanna at Loudetia	Bare soil	0,58	0,33	0,91
	Tussocks	1,66	2,19	3,85

TABLE I : Numerical abundance per mm^2

There is no evidence of differences between the two levels of the soil cores. Indeed, in the savanna at Hyparrhenia, 1,22 individuals per mm^2 has been found, on the surface and 1,25 per mm^2 in the depth ; in the savanna at Loudetia 1,12 per mm^2 on the surface and 1,26 per mm^2 in the depth. The paucity of the substratum in organic matter explains this uniformity of the vertical distribution.

C - Influcence of the roots (Table I)

The influence of the roots is more evident. The density in the tussocks reaches 3,22 living individuals per mm^2 in the savanna at Hyparrhenia and 3,88 per mm^2 in the savanna at Loudetia whereas, on bare soil, it reaches 1,71 per mm^2 in the savanna at Hyparrhenia and 0,91 per mm^2 in the savanna at Loudetia. The roots constitute, indisputably, a more significant biotop for the Testacea. Several factors may contribute to the biological activity of this region :

1) the higher content of nutrient elements
2) the protection from fire
3) these microhabitats are not affected by erosion
4) the microclimates are favourable and protected against dessication.

The bare soil is colonized by the populations which live in tussocks but this colonization is arrested periodically by the successive perturbations of fire or erosion. This explains the low likelihood that the populations reach equilibrium densities and the fact that only a few pionneer species occupying these habitats. Under these conditions a fine interactive community will not be established.

D - The empty tests

The proportions of the living and empty tests is of interest since it indicates, to some extent, the speed of the population turnover. In the biotopes where the degradation is fast, the proportion of empty tests is low. In the savanna at Hyparrhenia, it is very high and a little lower in the savanna at Loudetia. The high values are correlated with the effect of the fire because the living individuals are killed and it does not damage the majority of the empty tests. Therefore the production of empty tests by the action of fire is more important than in a normal biotope without for all that, implicating the speed of their elimination.

The source of the empty tests is as often as not local, any tests come from next microbiotopes carryed away by the wind or the run-off.

E - Biomass (Table II)

		a	b	a + b
Savanna at *Hyparrhenia*	Bare soil	0,14	0,04	0,18
	Tussocks	0,11	0,08	0,19
Savanna at *Loudetia*	Bare soil	0,05	0,02	0,07
	Tussocks	0,33	0,66	0,99

TABLE II : Biomass (kg per ha)

The total biomass reaches 0,183 kg per ha in the savanna at *Hyparrhenia* and 0,532 kg per ha in the savanna at *Loudetia*. These values are low in comparison with the other animals. In the savanna at *Hyparrhenia*, there is almost no difference between the tussocks and the bare soil whereas, in the savanna at *Loudetia*, the biomass in the tussocks reaches almost 1 kg per ha even though, between the tussocks, there are negligible protozoan population densities.

F - Diversity (Table III)

	a	b	Bare soil	Tussocks	total
Savanna at *Hyparrhenia*	2,10	1,31	1,12	2,30	2,50
Savanna at *Loudetia*	2,48	1,64	1,51	1,82	2,98

TABLE III : Diversity (Margalef's Index)

The diversity, calculated with the Margalef's Index is low in the both savannas. It is, in general, higher on the surface and in the tussocks and, on all the populations, in the savanna at *Loudetia* than in the savanna at *Hyparrhenia*.

IV - DISCUSSION AND CONCLUSIONS

In the both savannas, ressemblances exist at the level of the structural characteristics of the communities : the number of species, individuals, biomass and diversity. In all the parameters the tussocks are higher than the bare soil. It seems that the structural characteristics of the savanna protozoan species assemblage are principally determined by the low nutrient status of the soils and their morphological instability.

It is known that exposed biotopes are not favourable for the Testacea (COUTEAUX, 1976c) because they offer little protection and are liable to intense evaporation from the superficial layers where the Testacea are living. It might be expected that the hydrous system would be accountable for this effect as studies on the water-table in the forest of Sénart (France) have shown (COUTEAUX, 1976d). But this extreme low local abundance must be attributed to another factor. Indeed it has been shown, in France and in French Guiana (COUTEAUX, 1976a, 1977 and 1979 ; BETSCH and al., 1979) that the fire entirely destroys the Thecamoebian fauna in the first centimetres of the soil because the soil Protozoa are not capable of rapid migration to refuge microhabitats. In this case, the roots of the herbous tussocks can be considered as refuge zones from which the bare spaces are colonized.

This phenomenon is slow however that a stable species association is never established at low population densities. It is, therefore, concluded that the energetic participation of the Testacea to the ecosystem of burnt savanna is very low and localised in the roots of grass tussocks.

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EFFETS A COURT TERME DE LA DEFORESTATION A GRANDE ECHELLE DE LA FORET DENSE HUMIDE EN GUYANE FRANCAISE SUR LA MICROFAUNE ET LA MICROFLORE DU SOL

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INTRODUCTION

Devant l'ampleur du programme initialement prévu (600.000 ha en 15 ans) de déforestation à des fins papetières de la forêt guyanaise, la D.G.R.S.T. (Délégation Générale à la Recherche Scientifique et Technique - Gestion des ressources naturelles renouvelables) a incité 4 organismes de recherches fondamentales et appliquées (C.T.F.T., I.N.R.A., Muséum, O.R.S.T.O.M.) à effectuer une étude pluridisciplinaire des conséquences écologiques de l'exploitation et de la transformation de la forêt tropicale humide de Guyane. Cette action comporte deux aspects principaux :

- L'étude du recru naturel sur une parcelle expérimentale (dite "Arbocel") de 25 ha coupée à blanc en 1976 dans des conditions identiques à celles de l'exploitation papetière (180m^3/ha environ, soit 40% de la biomasse végétale restent sur place ; GUIRAUD, 1979) ; c'est cet aspect qui sera développé ici ;
- L'étude de l'installation d'écosystèmes simplifiés (pâturage, arboriculture fruitière, reboisements monospécifiques, ...) sur 8 bassins versants associés à 2 bassins témoins (B.V.A à J, de 1 à 1,5 ha en moyenne) ; ces manipulations de l'écosystème forestier ont débuté en 1978, après deux années d'étalonnage sous conditions naturelles.

La station expérimentale de Guyane se situe dans la zone équatoriale (5°30' lat. N ; 53° long. W) ; la pluviosité moyenne est estimée à 4.000 mm, avec une saison relativement sèche d'août à novembre, la température moyenne étant de 28°C.

Dans la parcelle Arbocel, la couverture pédologique, sur schistes Bonidoro, (HUMBEL, 1978) est constituée en grande partie de plateaux dont les sols sont à horizon humifère très peu épais et à cheminement de l'eau superficiel et latéral et de quelques bas-fonds hydromorphes. Le pH est compris généralement entre 4,3 et 5. La forêt dense humide avoisinante a une production de litière annuelle de l'ordre de 8,5 T/ha (PUIG, sous presse).

METHODES

Dans la parcelle Arbocel de 25 ha (Fig. 1), deux transects stationnels ont été retenus, l'un, T_1 sur sols drainés, l'autre, T_2 en bas fond hydromorphe ; les prélèvements ont lieu à 50 m à l'intérieur de la forêt (témoin ; - 50), à 50 m de la litière à l'intérieur de la parcelle (+ 50) et vers son centre (+ 300 sur T_1 ; + 200 sur T_2). Le feu ayant ravagé dès 1976 une partie de l'abatis, cette situation (très courante en Guyane) a fait l'objet d'une étude comparative en particulier en T_1 + 50 NB (non brûlé) et T_1 + 50 B (brûlé). De même, il a paru utile d'étendre la prospection aux chemins de halage du bois par les engins mécaniques (240 m/ha), mais le niveau "zéro" du sol n'est pas comparable à celui des autres biotopes, étant donné l'arrachement mécanique au cours du débardage et l'érosion consécutive.

Les prélèvements pour la microfaune, la matière organique, la rétention hydrique et les mesures d'activité respiratoire ont lieu aux niveaux suivants : litière (éventuellement), H_1 (0-1 cm), H_2 (-1-3,5 cm), H_3 (-3,5-6 cm), H_4 (-6-8,5 cm).

Les résultats ne pouvant tous être présentés, nous nous sommes souvent limités aux comparaisons des 4 situations les plus représentatives de la parcelle, sur le transect n° 1 (sol draîné) :

- 1 : forêt-témoin ; T_1 - 50
- 2 : abatis non brûlé ; T_1 + 50 NB
- 3 : abatis assez fortement brûlé ; T_1 + 50 B
- 4 : chemin de halage ; CH.

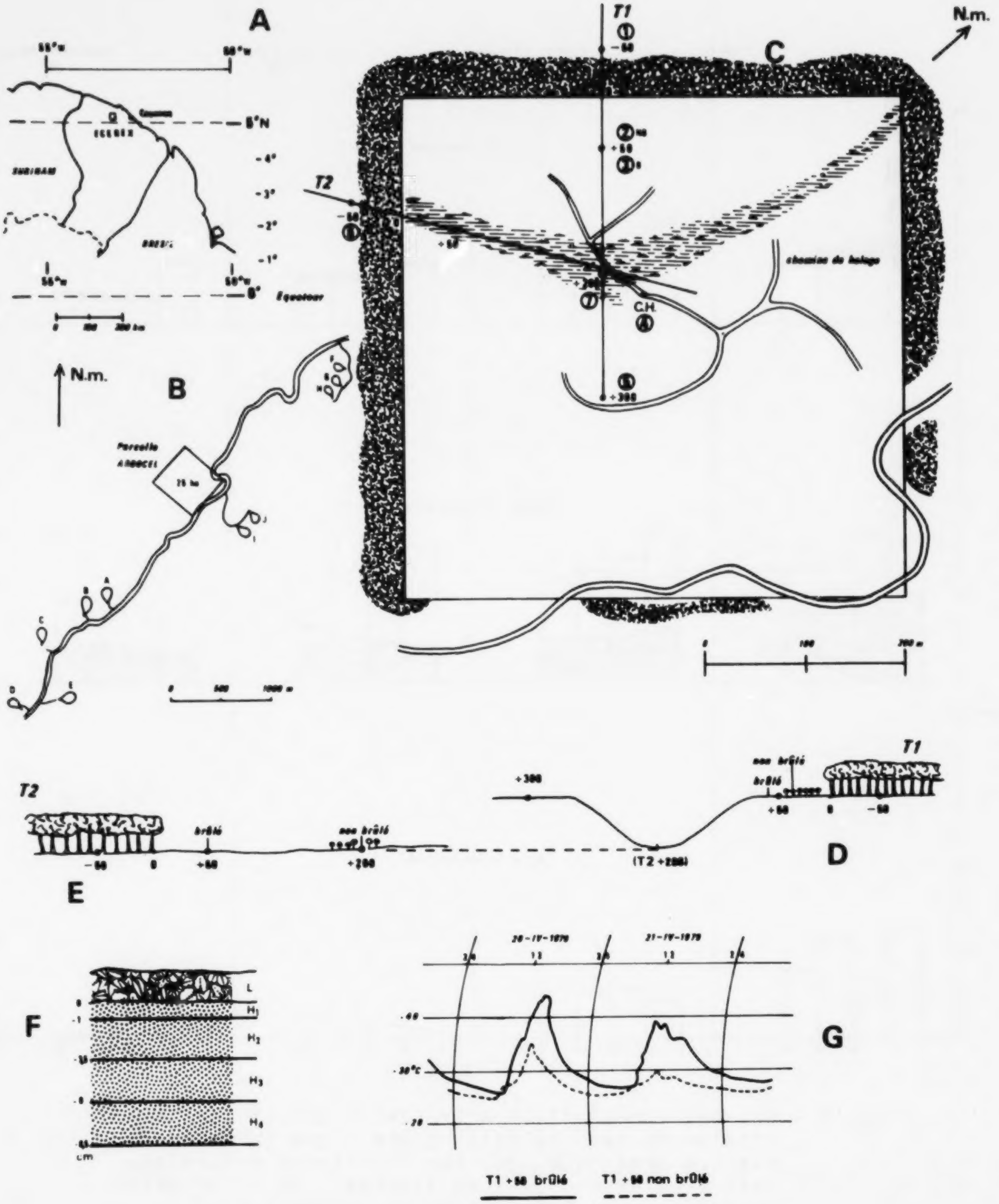
Dans les abatis non brûlés, la couverture végétale composée d'espèces pionnières à pousse très rapide, essentiellement Cecropia et Goupia, atteint 4 m de hauteur deux ans après la coupe. Sur les abatis assez fortement brûlés et les chemins de halage, la végétation était alors inexistante. Les températures enregistrées dans le sol (exemple à - 1 cm ; Fig. 1) sont nettement plus élevées dans les biotopes découverts que dans l'abatis avec recru naturel.

RESULTATS

I - Matière organique :

La méthode de dosage du carbone selon Anne n'étant bien appropriée que pour des sols dont le taux ne dépasse pas 3%, nous avons adopté la méthode d'attaque par $H_2 O_2$ à chaud, donnant le taux de matière organique totale par différence de pesée du sol sec. Cette analyse est complétée par une séparation par flottation des éléments figurés incomplètement biodégradés surnageants et de la matière

Fig. 1 - A. - Situation de la parcelle expérimentale en Guyane Française. B. - Dispositif expérimental pour l'étude de la déforestation et des manipulations de l'écosystème. C. - Parcelle expérimentale et situation des stations de prélèvements sur les transects. D. - Coupe schématique du transect 1. E. - Coupe schématique du transect 2. F. - Coupe schématique du sol montrant les différents horizons étudiés et leur profondeur. G. - Courbe de température à -1 cm dans le sol dans les abatis brûlé et non brûlé à T_1 + 50.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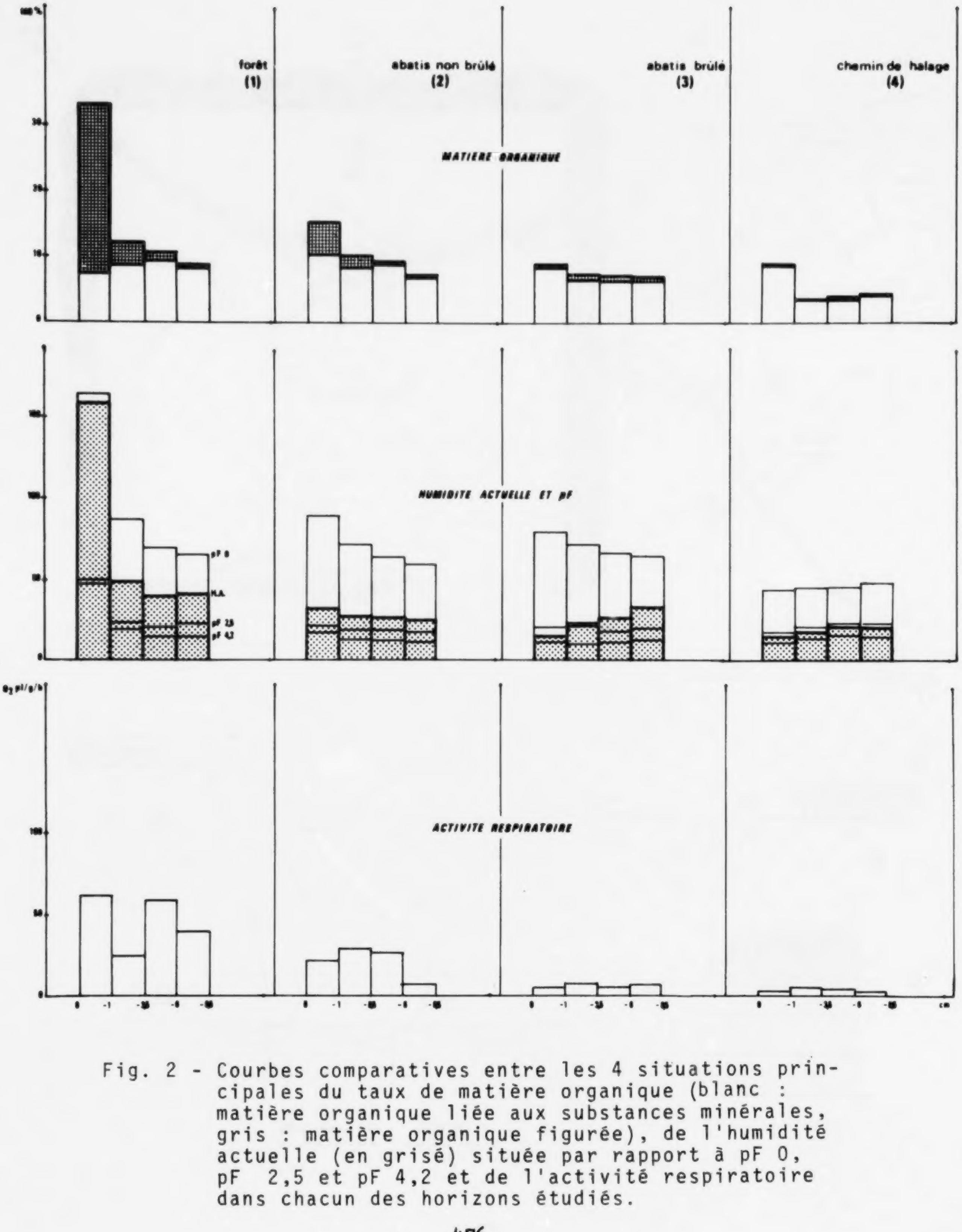


Fig. 2 - Courbes comparatives entre les 4 situations principales du taux de matière organique (blanc : matière organique liée aux substances minérales, gris : matière organique figurée), de l'humidité actuelle (en grisé) située par rapport à pF 0, pF 2,5 et pF 4,2 et de l'activité respiratoire dans chacun des horizons étudiés.

organique liée aux substances minérales, en particulier aux argiles.

De ces analyses, on peut tirer les conclusions suivantes (Fig. 2 et 3) :

- les taux de matière organique sont très élevés puisqu'ils varient entre 33% et 9% dans les horizons supérieurs et atteignent encore 7% dans les horizons -6-8,5 cm.
- le taux de matière organique total décroît de la forêt à l'abatis non brûlé, puis à l'abatis brûlé. Mais cette diminution porte surtout sur les deux premiers horizons (0 à -3,5 cm) et affecte principalement la matière organique surnageante. Les taux de matière organique liée aux substances minérales varient peu d'un sol à l'autre, quel que soit le traitement subi, deux ans après la déforestation.
- les taux de matière organique du chemin de halage peuvent surprendre mais il faut tenir compte du stock existant, des apports lors du débardage et par le ruissellement. Par contre, le taux de surnageant est très faible en l'absence de végétation.
- on constate un enrichissement des sols sous couvert entre mars 1977 et avril 1978, surtout en matière organique surnageante qui peut provenir de la chute de litière des espèces recolonisatrices dans les abatis non brûlés, mais aussi d'un phénomène saisonnier puisqu'il apparaît aussi en forêt (les prélèvements ne sont pas exactement superposés dans le cycle annuel).

II - Rétention hydrique :

Les humidités actuelles des sols relevées au moment des prélèvements pour la microfaune, la microflore et l'activité respiratoire ont été comparées aux humidités de ces mêmes sols soumis sous presse à membrane à pF 0, pH 2,5 et pF 4,2.

La figure 1 illustre les comportements hydriques dans les 4 situations-types en sols drainés :

- la forêt-témoin et l'abatis non brûlé présentent une décroissance de l'humidité actuelle de leur sol avec la profondeur, ce phénomène étant évidemment très accentué dans la forêt climacique. Les courbes d'humidité aux trois valeurs référence de pF suivent la même tendance.
- l'abatis brûlé voit l'humidité actuelle de son sol croître avec la profondeur et ceci quel que soit le moment de la dernière précipitation (10 minutes ou 2 jours). Il est remarquable que les courbes d'humidité aux trois valeurs référence de pF ne suivent pas cette tendance ; dans les deux horizons superficiels, l'humidité correspond à des pF supérieurs à 2,5 et même proche de 4,2 en surface.

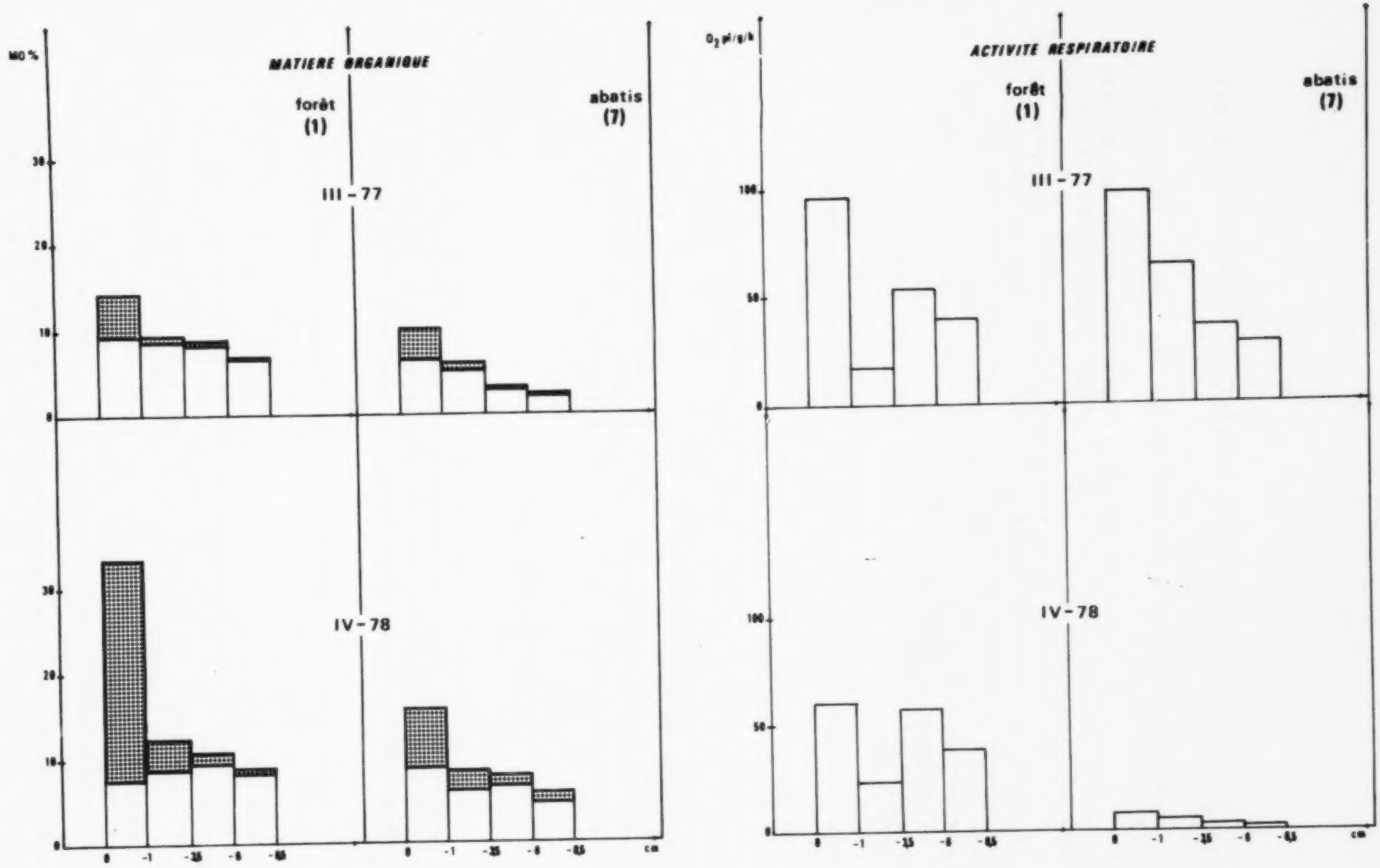


Fig. 3 - Courbes comparatives de l'évolution du taux de matière organique et de l'activité respiratoire des sols entre mars 1977 et avril 1978, en forêt témoin et dans un abatis.

- le chemin de halage présente une humidité croissant avec la profondeur, mais qui est ici en accord avec les courbes aux trois valeurs référence de pF.

III - Microfaune du sol :

1 - Thécamoebiens

L'échantillonnage a porté en 1977 sur l'abatis T_1 + 300 B (5) et les abatis non brûlés T_1 + 300 NB sans litière (8) et avec litière (9), et en 1978 sur les stations 1, 2 et 3 (voir figure 1).

Quatorze espèces ou variétés ont été trouvées sous forme d'individus vivants dans les stations indiquées : *Centropyxis sp*.(1), *Cyclopyxis kahli* (2), *Euglypha laevis* (1), *Euglypha rotunda* var. *minor* (ou *E. capsiosa* ou *E. hyalina*) (1), *Hyalosphenia subflava* (50 µm ; 9), *H. subflava* (100 µm ; 9), *H. subflava* (135 µm ; 2), *Nebela militaris* (9), *Phryganella acropodia* (1,5, 8, 9), *P. acropodia* var *penardi* (1,9), *Trinema complanatum* (9), *T. enchelys* (9), *T. grande* (1,9), *T. lineare* (9).

L'estimation de la densité sur 2 cm de profondeur varie entre 1,14 et 21,49 individus vivants au mm^2, la biomasse de 0,12 à 1,71 kg/ha.

L'abatis non brûlé où, de plus, la litière est en place est le biotope le plus riche tant pour le nombre d'espèces que pour le nombre d'individus. Sur la base des données préliminaires dont nous disposons actuellement, il n'y a pas de différence significative entre ce type d'abatis et la forêt-témoin. La couverture de litière et, pour 1978, la recolonisation par les *Cecropia* confèrent à ce biotope un caractère abrité qui s'apparente à un milieu forestier (COÛTEAUX, 1979).

Par contre, en abatis brûlé, les niveaux de surface sont dépourvus de Thécamoebiens. Cet effet néfaste du feu, déjà observé en France et en Côte d'Ivoire (COÛTEAUX, div. publ.), intervient par l'élévation de la température, la modification chimique du milieu, l'érosion des couches superficielles qui sont les seules à abriter des Thécamoebiens et la modification de la disponibilité hydrique.

Il existe environ 3 fois plus de thèques vides que d'individus vivants. Cette proportion, faible par rapport à ce qui a été trouvé en forêt tempérée humide ou en savane tropicale (COÛTEAUX, div. Publ.), peut témoigner d'un turn-over plus rapide.

2 - Microarthropodes du sol

Les résultats quantitatifs globaux concernent une période sensiblement identique au cours des années 1977 et 1978 (en pleine saison des pluies) où les populations sont à leur effectif et à leur diversité maxima. Les autres prélèvements, en août ou novembre, ne montrent pas de modification spectaculaire de ces deux données (environ 60% des effectifs maxima).

- Effectifs globaux :

La figure 4,A donne le niveau des populations de microarthropodes du sol dans les 4 horizons étudiés et éventuellement, dans la litière, 20 mois après la coupe à blanc de la forêt. Les deux types de forêt-témoin, et, dans une mesure à peine moindre, l'abatis non brûlé sur sol hydromorphe, renferment des populations nombreuses à presque tous les niveaux du profil (à remarquer que les chiffres ne donnent pas une bonne idée de la biomasse dans la litière où la taille des individus est nettement plus forte que dans le sol). Tous les autres sols ayant subi un traitement présentent des populations peu nombreuses ; l'abatis fortement brûlé n° 3 est même totalement dépourvu de faune dans son horizon supérieur.

L'évolution des effectifs de l'abatis non brûlé n° 2 entre mars 1977 (litière au sol provenant des arbres abattus) et avril 1978 (litière de Cecropia et Goupia, du recru naturel) montre une stabilité numérique des populations dans la litière mais une chute très marquée des effectifs dans le sol (Fig. 4, B). De même, l'abatis brûlé n° 5 voit sa population se réduire deux ans après la coupe à blanc.

A cette diminution très forte des effectifs s'ajoute une diversité très réduite des groupes zoologiques représentés dans les zones manipulées.

- Rapport Acariens/Collemboles :

Ce rapport, généralement utilisé pour un sol total (cf. en particulier MALDAGUE, 1961), est en réalité très variable selon les horizons du sol. La figure 4, C montre que ce rapport présente une courbe ascendante assez voisine dans les deux types de forêt-témoin, mais aussi dans l'abatis non brûlé sur sol drainé, et, avec une amplitude bien moindre, dans l'abatis non brûlé sur sol hydromorphe ; les deux abatis non brûlés, qui constituent la modification la moins accusée de l'écosystème, suivent donc assez bien les caractéristiques des sols des formations climaciques. Tous les autres sols manipulés présentent des courbes non interprétables actuellement.

- Analyse globale des Collemboles

Devant l'impossibilité de déterminer au niveau spécifique un nombre suffisant d'espèces de Collemboles (par manque de travaux systématiques exhaustifs), nous avons appliqué le critère différentiel d'ODUM aux 5 grands groupes: Néélipléones, Symphypléones, Poduromorphes, Isotomides et Entomobryens. Les relations entre les stations comparées deux à deux sont mises en évidence, de même que leur évolution relative entre mars 1977 et avril 1978. L'analyse n'a été effectuée que pour la litière et les deux premiers horizons (Fig. 4, D, E et F) ; en-dessous, la faiblesse des effectifs ne permet pas d'obtenir de résultat représentatif.

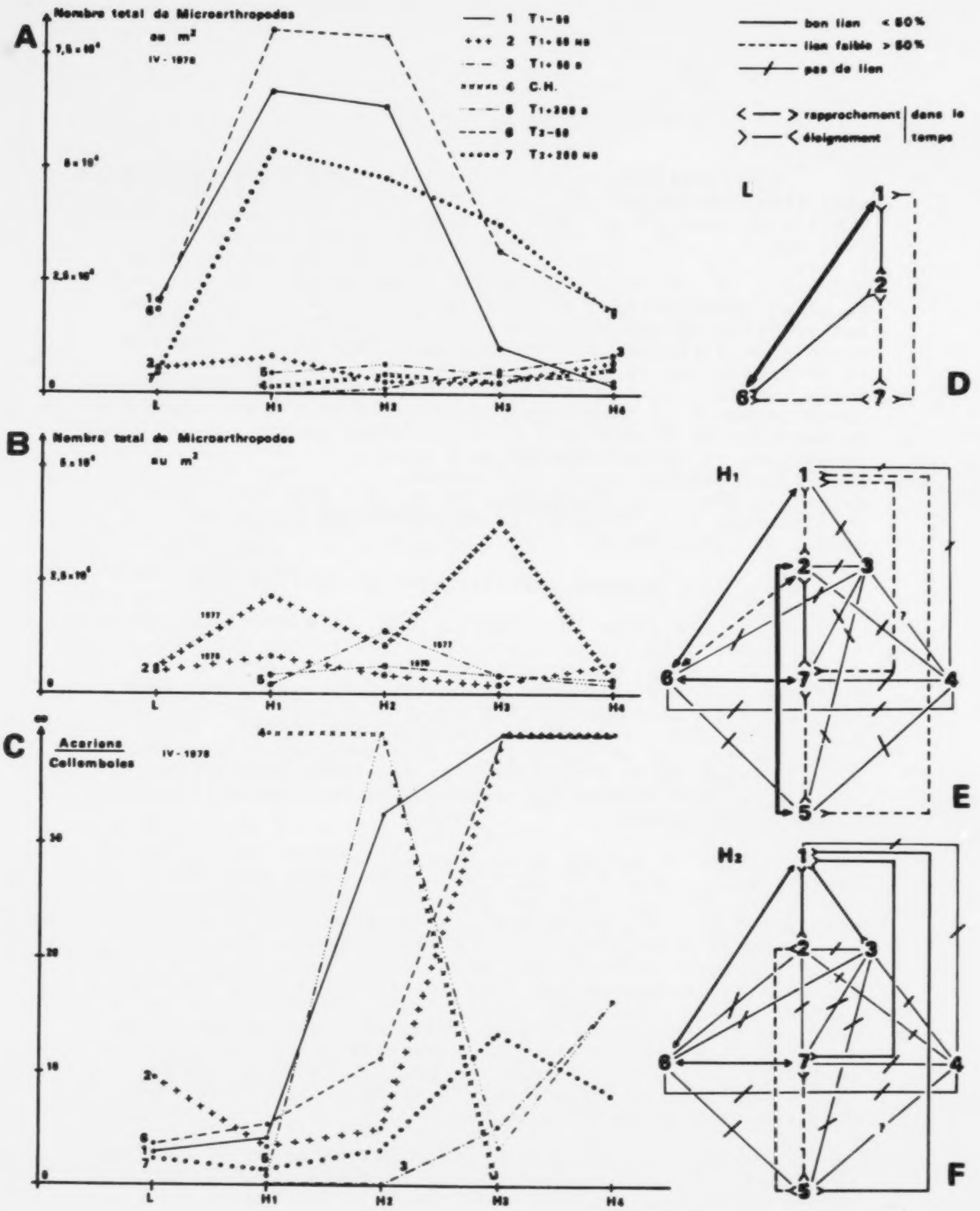
Les deux types de forêt-témoin sont évidemment bien liés, surtout dans la litière ; dans le sol, le caractère assez hydromorphe de la station 6 se répercute sur les valeurs du lien ; le léger rapprochement dans le temps semble dû à la phénologie du climat un peu différente en 1978.

En ce qui concerne les zones modifiées, il faut remarquer immédiatement l'isolement total de l'abatis fortement brûlé (3 ; sauf à partir de H_2, mais avec éloignement) et du chemin de halage (4) ; l'abatis non brûlé sur sol drainé (2) conserve dans l'ensemble de bons liens avec son témoin (1), mais s'en éloigne à tous les niveaux. L'abatis brûlé n° 5 présente de bons ou assez bons liens avec l'abatis non brûlé n° 2 dont il se rapproche même en surface après l'éloignement initial dû au traitement subi ; mais ses liens comparés avec l'abatis non brûlé (2) et l'abatis fortement brûlé (3) montrent qu'il existe moins de différence entre le non brûlé et le faiblement brûlé qu'entre ce dernier et le fortement brûlé. Quant à l'abatis non brûlé sur sol assez hydromorphe (7), il s'écarte de son témoin (6) pour la litière, mais s'en rapproche pour les horizons du sol, avec un lien moyen à bon.

- Données qualitatives sur les Collemboles Symphypléones.

Ce groupe essentiellement épigé est intéressant par les renseignements qu'il peut donner sur les caractéristiques du biotope, qu'il soit forestier primaire, secondaire ou découvert. La litière de la forêt-témoin sur sol drainé (1) renferme les genres typiques de forêt comme *Temeritas*, *Collophora*, *Pararrhopalites*, *Neosminthurus* et *Sphyrotheca* auxquels s'ajoutent, à l'état dispersé, les Dicyrtomidae. En 1977, la litière de l'abatis non brûlé (2) ne renfermait que des Dicyrtomidae qui sont caractéristiques des forêts secondaires en zone intertropicale ; en 1978, une partie du contingent de Symphypléones de forêt primaire était déjà présent dans la litière du recru naturel de ce même abatis : *Sphyrotheca* et *Pararrhopalites* qui s'étaient adjoints aux Dicyrtomidae.

Fig. 4 - A. - Evolution du nombre total de microarthropodes du sol en fonction de la profondeur dans les différentes stations. B. - Evolution du nombre total de microarthropodes entre 1977 et 1978 dans les stations 2 et 5. C. - Evolution du rapport Acariens/Collemboles en fonction de la profondeur dans les différentes stations. D, E et F. - Schéma des relations entre les stations et de leur évolution basé sur le critère différentiel d'ODUM appliqué aux Collemboles (D, litière ; E, horizon H_1 ; F, horizon H_2).



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IV - Microflore du sol :

L'élimination partielle ou totale des microorganismes peut être considérée comme un facteur de la mesure de l'activité biologique, mais la suppression des germes, contrairement à celle de la faune, entraîne des phénomènes irréversibles. La microflore saprophytique du sol, au même titre que la photosynthèse et les éléments géochimiques, est en effet indispensable au maintien de la vie sur terre, car son activité métabolique permet le recyclage des éléments organiques élaborées par les plantes. Même si les effets de la déforestation ne sont pas drastiques, l'éclipse d'une flore spécifique, la cellulolytique par exemple, empêchera temporairement le déroulement d'un cycle vital, en retardant la dégradation microbienne d'un composant majeur des cellules végétales, le polysaccharide en l'occurence. La fragilité des sols tropicaux étant bien connue, le blocage ou le freinage d'un processus biologique de ce type peut avoir des conséquences très néfastes en contrecarrant les futurs essais de reboisement.

1 - Données quantitatives et qualitatives.

Deux ans après la déforestation, la microflore totale ne varie que très peu au cours de la saison des pluies (KILBERTUS, 1979). Mis à part une station en pente qui présente un appauvrissement en germes par rapport aux sols forestiers correspondants (1,5 contre 3,4 x 10^6 germes/g de sol), dans toutes les autres stations, les chiffres sont compris entre 3,2 et 4,8 x 10^6 microorganismes par gramme de sol. Etant donné l'imperfection des techniques de numération, ces différences ne peuvent être considérées comme étant significatives.

Durant la saison sèche, les différences sont plus importantes : selon les stations,les moyennes vont de 1 à 28,2 x 10^6 bactéries par gramme de sol. Seule la station brûlée (3) et celle du talweg (7) renferment des quantités de microorganismes comparables à celles des milieux boisés (respectivement 10,8 et 28,2 pour 12,9 - 9,2 - et 18,6 x 10^6 cellules par gramme de sol dans les stations boisées). Ces deux parcelles présentent une écologie particulière : la première (3) est très riche en éléments minéraux résultant de la calcination des arbres, la seconde (7) située dans un talweg, reste constamment humide (KILBERTUS et PROTH, 1978). Ces particularités permettent en partie d'expliquer leur composition microbiologique.

Du point de vue qualitatif, l'élimination de la forêt se traduit par une raréfaction ou une disparition de certaines espèces caractéristiques des biotopes boisés :

- dans les stations de plateau, les Micrococcus disparaissent ou diminuent sensiblement en nombre dans les parcelles déboisées. Par contre, les différentes espèces appartenant au genre Arthrobacter résistent très bien. Les mêmes remarques s'appliquent aux stations de pente.

- dans les stations de talweg, Bacillus licheniformis toujours présent dans les sols forestiers, n'apparait plus dans les zones déforestées. Il est intéressant de noter que dans ces dernières, certains germes caractéristiques des parties moins humides (Arthrobacter et Bacillus brevis) sont isolés au cours de la saison sèche.

Ces modifications qualitatives semblent caractériser un stade transitoire, la durée de l'élimination des arbres étant insuffisante pour provoquer la disparition totale de certains microorganismes telluriques.

Signalons enfin que la composition qualitative de la mycoflore ne semble être guère affectée (KILBERTUS, 1979).

2 - Apports de la microscopie électronique :

La microscopie électronique apporte des données complémentaires :

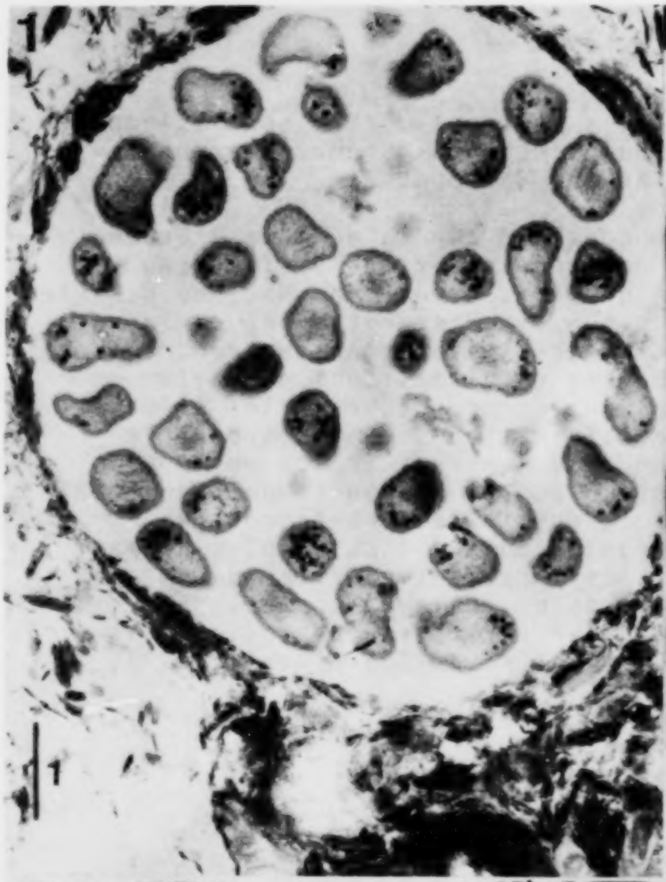
- elle confirme que les sols dépourvus de strate arborée, même ceux des chemins de charriage, continuent à renfermer des bactéries vivantes, généralement protégées par les argiles.
- Les colonies de procaryotes, lorsqu'elles sont visibles, se présentent souvent sous forme d'amas de cellules englobées dans un mucilage à la surface duquel s'adsorbent des feuillets d'argile (Fig. 5, 1). Le polysaccharide et les phyllosilicates jouent un rôle important et leur présence explique la survie des germes au cours de périodes défavorables (KILBERTUS et coll., 1977).
- ces colonies bactériennes sont abondantes dans les sols forestiers au cours de la saison sèche, mais elles sont remplacées par des formes isolées durant la période humide. La station boisée de talweg renferme d'ailleurs essentiellement des procaryotes isolés, ce qui semble confirmer l'influence des saisons.

Par contre, dans les parcelles sans arbre, c'est au cours de la saison humide qu'apparaissent les associations de bactéries, la saison sèche étant caractérisée par des formes à l'état de vie latente, rétractées à l'intérieur du mucilage.

- chaque station renferme des germes à ultrastructure particulière, comme celui représenté dans la figure 5,4.

Fig. 5 - Microflore du sol ; clichés au microscope électronique à transmission. Les échelles sont données en µm. Les coupes ont été contrastées selon la technique de Reynolds (R) ou de Thiéry (T).
- 1, colonie bactérienne dans un sol forestier (T).
- 2 et 3, germes isolés rencontrés dans les stations déboisées (R). - 4, germe particulier rencontré dans une station déboisée en pente (R).

1



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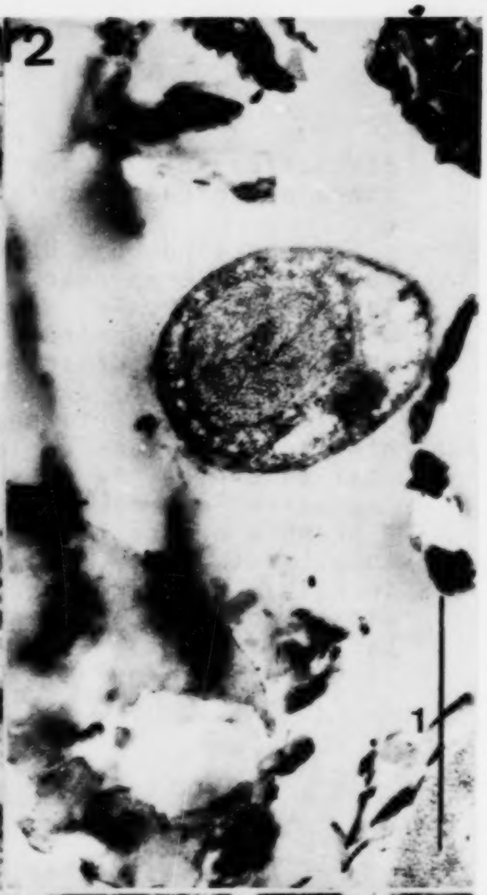

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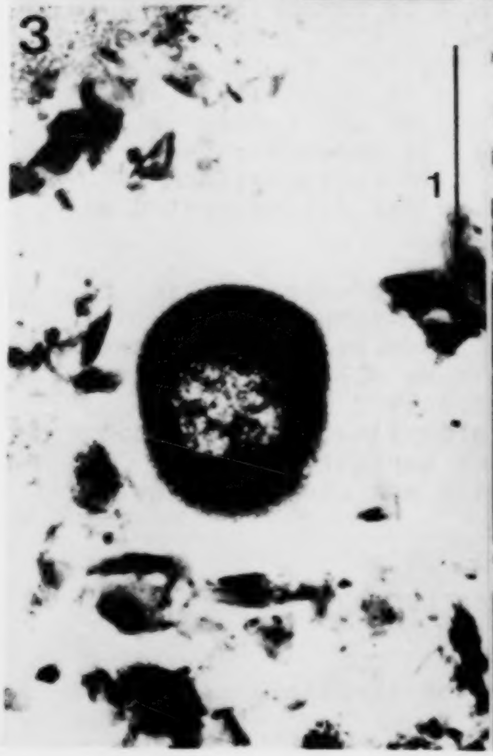

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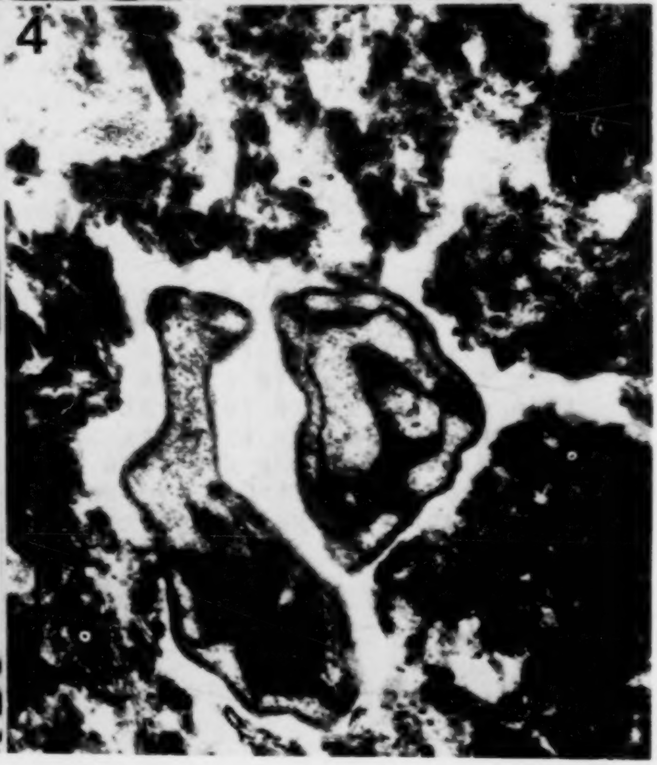

- enfin, les stations 3 et 7 se distinguent des autres sols par des quantités plus importantes de matière organique imparfaitement décomposée.

Nous pouvons donc conclure que la période d'étude nous semble trop courte pour provoquer des différences tranchées entre les stations boisées ou non. Mais on assiste néanmoins à la diminution ou à la disparition de certains procaryotes aux dépens d'espèces mieux adaptées aux nouvelles conditions de vie. Ces résultats sont dûs à la persistance de certaines sources trophiques : les éléments minéraux résultant de la calcination des arbres dans la station brûlée, la présence de nombreux troncs morts dans les parcelles non brûlées. D'autres facteurs sont également à prendre en compte, car le chemin de débardement (4) totalement dépourvu de végétation n'est pas biologiquement inactif. Les microorganismes possèdent en effet des mécanismes de protection (endospores, chlamydospores, protection par les argiles, ...) qui leur permettent de résister durant les périodes défavorables (KILBERTUS et coll, 1978, 1979).

V - Activité respiratoire des sols :

Les sols séchés, tamisés à 2 mm, sont remouillés à pF 3 ; ils sont maintenus 7 jours à la température d'incubation retenue (29°C en général ; 45°C pour certains sols découverts, compte tenu des élévations de température qui y ont été relevées). La mesure de la respiration est réalisée à pression constante sur 5 g de sol (poids sec). Le CO_2 étant absorbé par la potasse, la dépression dans la chambre respiratoire correspond à la consommation d'oxygène potentielle que l'on mesure par déplacement d'un index dans un tube capillaire.

En sols drainés, la consommation d'oxygène (Fig. 2) décroît de manière sensible de la forêt-témoin (1) à l'abatis non brûlé (2), et dans des proportions très fortes dans l'abatis brûlé (3) et le chemin de halage (4). L'évolution de l'activité respiratoire entre 1977 et 1978 est illustrée par deux exemples : la forêt-témoin (1) ne voit de modification que dans son horizon supérieur tandis que l'abatis non brûlé (7) enregistre une chute remarquable de son activité respiratoire.

DISCUSSION - CONCLUSION

Il est difficile de dégager une stratégie commune pour l'ensemble des fonctions d'un biotope donné. En effet les microorganismes telluriques peuvent être présents dans un sol fortement modifié par leurs formes de résistance ce dont les microarthropodes du sol sont géneralement incapables ; de même, l'activité de la microflore peut être importante alors que les microarthropodes peuvent alors être relativement peu nombreux.

Pour nous en tenir aux quatre situations principales sur sol draîné consécutives au déboisement, les grandes lignes dégagées par nos observations sont les suivantes :

- le sol de la forêt climacique présente une forte teneur en matière organique, une forte capacité de rétention hydrique, des populations de microarthropodes nombreuses et diversifiées, des populations importantes de microorganismes principalement sous forme de colonies, un niveau élevé d'activité respiratoire.
- dans l'abatis non brûlé, les principales modifications concernent le niveau assez faible des populations de microarthropodes, une capacité de rétention hydrique plus réduite et un niveau assez faible d'activité respiratoire ; certaines données qualitatives chez les Collemboles permettent de dire que l'éloignement dans le temps de cette station par rapport au témoin peut connaître après deux ou trois ans un renversement de tendance.
- Les deux situations dramatiques représentées par une action importante du feu et celle des engins mécanisés de halage des bois voient pratiquement tous les domaines d'activité se dégrader dans de très fortes proportions. Les niveaux relativement élevés d'activité microbienne sont à mettre de manière pratiquement certaine en rapport avec le stock de source trophique encore disponible ou amenée par la calcination des bois. Mais, les données qualitatives montrent que ces deux types de biotopes sont en équilibre instable et risquent, par une prolongation de la suppression de couvert végétal, de devenir irréversiblement impropres à la régénération de la végétation.

REMERCIEMENTS

Nous remercions très vivement Mrs. Francis DEVAUX, Yann MIKHALEVITCH et Frédéric SEVOZ pour leur précieuse aide technique et l'exploitation des données.

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QUESTIONS and COMMENTS

H. KOEHLER: Can you say anything about the reestablishment of trophic structures (Carnivores, phytophages and detritophagous organisms) on the cleared plot?

J.-M. BETSCH: Actually, only general aspects and certain particular data concerning the relations between different habitats have been analysed. Moreover, data of natural regrowth are available for only the first two years; these data are not yet sufficient to allow us to describe the stages of reestablishment of trophic structures.

RELATIONSHIPS OF SOME ISOTOMIDAE (COLLEMBOLA) WITH HABITAT AND OTHER SOIL FAUNA

*Penelope Greenslade and **P. J. M. Greenslade

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INTRODUCTION

One might expect competitive interactions to play a significant part in population processes of microarthropods and other invertebrates inhabiting the soil since they live in diverse communities in a sheltered environment. This applies especially in the humid tropics where ground layer invertebrate faunas are very rich and the climate is equable and favourable (Bullock, 1967). One would also expect competition to be diffuse (Terborgh, 1971; MacArthur, 1972), with any one species liable to interact with a patchwork of others at varying densities and in varying combinations. Competitive interaction of this sort has been described by Kaczmarek (1975a,b) in Polish pine forests. The distributions and densities of 'Oligovalent' collembolan species (i.e. specialised in respect to habitat), depended to a large extent on moisture. The pattern of density of 'Polyvalent' species, with less specialised habitat requirements, varied inversely with the density of the more specialised ones. Kaczmarek concluded that the latter had a limiting effect on the unspecialised species. Their distributions could not be accounted for in terms of any one oligovalent species and so diffuse competition is indicated. Here we continue a re-examination of data on the soil fauna of the Solomon Islands in the light of recent ideas in ecology and report similar results. A previous paper dealt with the ants (Hymenoptera : Formicidae) of the same area (Greenslade and Greenslade, 1977).

AREAS STUDIED

Three sites were sampled on the north coast of Guadalcanal, Solomon Islands, in the southwest Pacific. They were situated amongst grasslands, coconut plantations and lowland tropical rain forest in an area with a moderately seasonal tropical climate.

Shifting cultivation sequence

A subsistence garden and adjacent forest provided three plots representing early stages typical of shifting cultivation:

(a) Forest that had not been recently disturbed and had a well developed litter layer.

(b) Bare ground immediately after clearing Forest. Trees had been felled and the trunks laid in a grid; other vegetation had been heaped up and burnt.

(c) A Garden of ca 0.3ha of sweet potato, (Ipomoea batatas Lam.), six months old which had been planted without general cultivation of the soil. The foliage gave a light ground cover and there was a thin litter layer.

Coconut plantation transect

A line of 18 square contiguous quadrats, each $0.37m^2$, was laid out across a vegetation discontinuity in a coconut plantation (Figure 3). Zone I consisted of grasses, 15cm deep in Zone Ia, reaching 1m near the base of a palm in Zone Ib. Zone II carried a sparse growth of Stachytarpheta sp. (Verbenaceae).

Plantation ground cover trial

Another coconut plantation was clean cultivated two years prior to sampling and divided into three blocks of 4ha, each of which was subdivided between three treatments.

(a) Cover Crop, Pueraria, up to 1m deep with a litter layer.

(b) Short Grass, recolonising grasses mown to maintain a sward 10cm deep.

(c) Long Grass, mown less frequently and reaching a height of 1m.

METHODS

Sampling

In the Solomon Islands the soil fauna is concentrated close to the surface (Greenslade and Greenslade, 1968) and large, shallow samples were used, 2.5 or 5cm deep, $275cm^2$ in area. Large area reduces variability caused by highly aggregated distributions and low average density of many individual species. Apart from mites and some immature Collembola all the extracted fauna was sorted to species, although, combined with the large size of the samples, this limited the number of samples that could be handled. Samples were taken at random as follows:

Shifting Cultivation Sequence:		Forest	Bare Ground	Garden
Litter	Depth	7	-	4
	0-2.5cm	7	5	4
Soil	5-7.5cm	4	4	4
	10-12.5cm	8	4	8

Plantation Transect : three samples per quadrat, 5cm deep.

Plantation Ground Cover Trial : litter samples (Cover Crop only), soil samples from 0 to 2.5cm and from 2.5 to 5cm at four points per plot.

Extraction

Samples were extracted in simple plastic funnels. Preliminary trials tested the effects of retaining samples within cylindrical

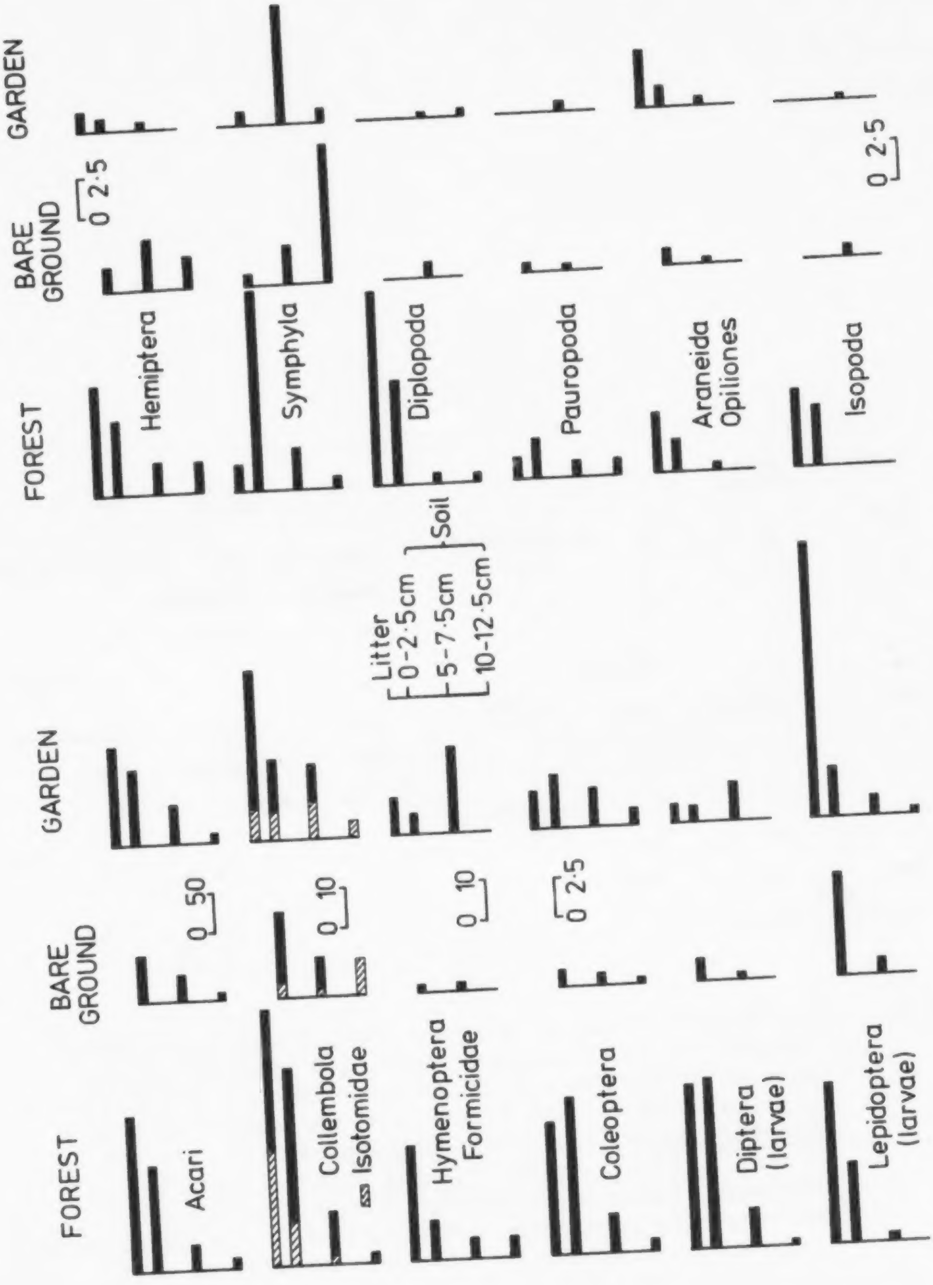

FIGURE 1. Shifting Cultivation Sequence, mean numbers per sample ($275cm^2$).

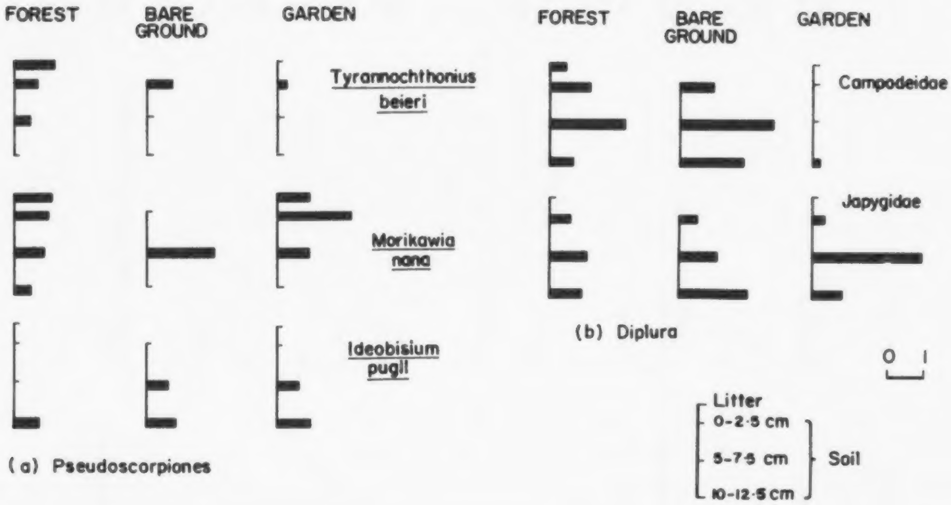

FIGURE 2. Shifting Cultivation Sequence, mean numbers per sample ($275cm^2$) of (a) pseudoscorpions, (b) Diplura. Five species of pseudoscorpion were recorded in the Forest samples, those in the Figure and one example each of a Smeringochernes and an Alocobisium species. In the order, T. beieri Beier, M. nana Beier, I. pugil, Morikawa, these three species form a sequence of decreasing pigmentation and reduction in ocelli as their distributions extend further into the mineral soil. Similarly, in the Diplura, the Campodeidae have long, fragile appendages and in the Solomon Islands are generally found near the soil surface and in litter (Manton 1972). The more robust Japygidae, with shorter appendages are more frequent in mineral soil.

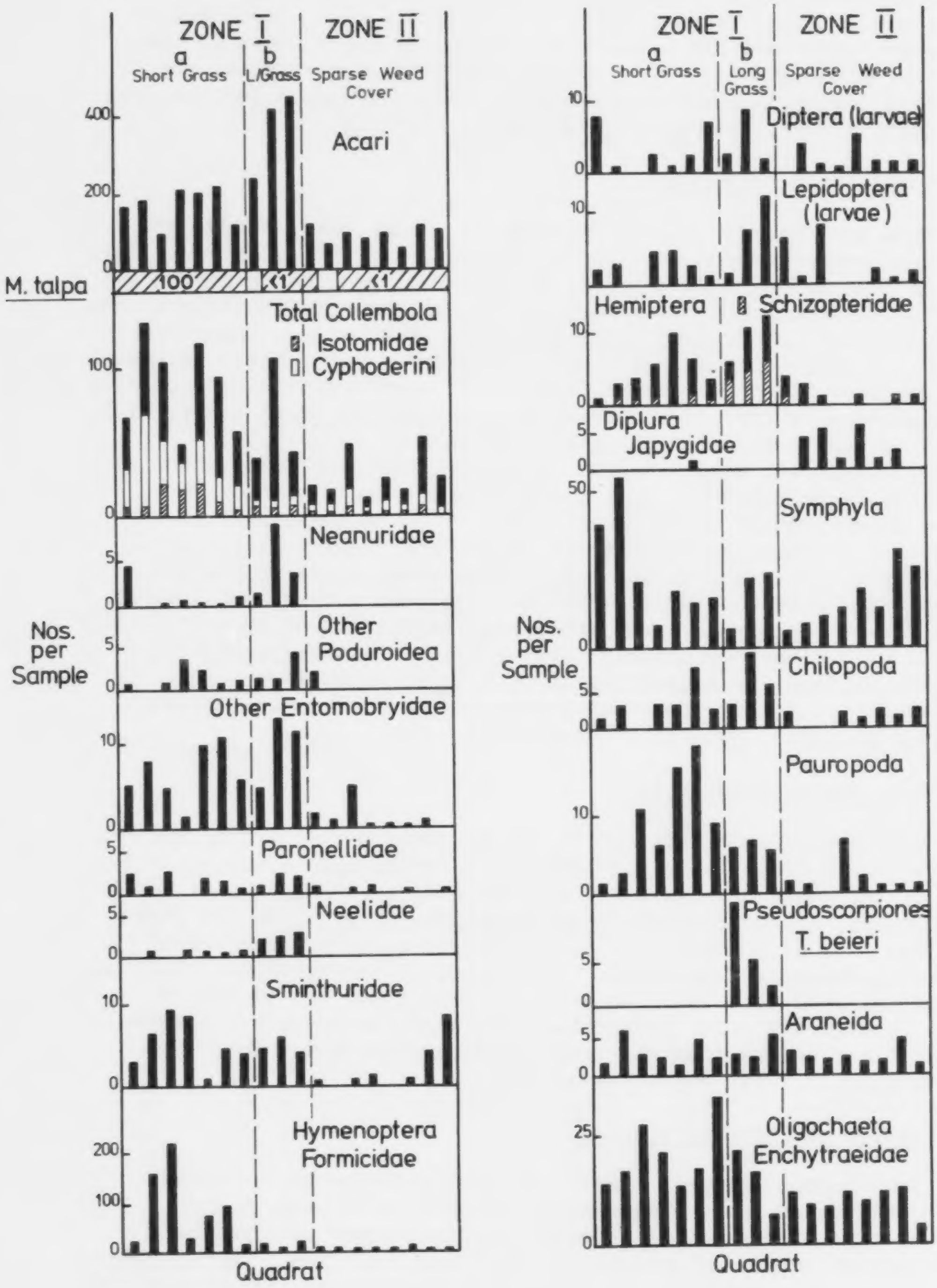

FIGURE 3. Coconut Plantation Transect, mean numbers per sample ($275 cm^2$), per quadrat. The distribution and numbers per sample of the ant, Monomorium talpa are shown below 'Acari'.

Forest levels of density and diversity were not regained. A few species of Cryptostigmatid mites were disproportionately abundant in samples from the Garden. The Coleoptera, Diptera and Hemiptera contain many species of varied function, usually with winged adults, and appropriately adapted species entered the cleared areas as the habitat became suitable. But, in the Coleoptera for example, the entry of a few open habitat Carabidae did not compensate for the loss of the many staphylinoid species occurring in Forest.

Coconut plantation transect

This area had not been cultivated and shows some effects of vegetation cover independently of other factors. The fauna under Tall Grass in Zone Ia had some forest-like features : maxima in neelid and neanurid Collembola and the presence of a schizopterid (Hemiptera) and the pseudoscorpion, *Tyrannochthonius beieri* (Figure 3). There was evidence of interactions with a well established ant fauna. In Zone I the numbers of mites in samples (log n + 1) were negatively correlated with numbers of a cryptic myrmicine ant, *Monomorium talpa* Emery, with a dense nesting population in Zone Ia (Figure 3) ($r = -0.54$, $p<0.001$). This ant also occurred in the Ground Cover Trial where it was widely distributed and here mites were obtained in about equal numbers from Long and Short Grass (Table 1). The numbers of cyphoderine Collembola, inhabitants of ant and termite nests, were positively correlated with total ants from samples over the whole Transect ($r = 0.64$, $p<0.001$). Two faunal elements that were present in the Garden reappeared under the sparse vegetation of Zone II of the Transect. They were groups with soil surface or above ground mobility, at least as adults (spiders, Opiliones, Diptera, Lepidoptera), and soil inhabitants able to escape from the surface climate (Japygidae, Symphyla) (Figure 3).

Plantation ground cover trial

Most groups were obtained in the greatest numbers from samples from the Cover Crop (Table 1, Figure 4). Forest-like elements of the fauna of the Cover Crop were Pselaphidae and, as in the Long Grass of the Transect, Neanuridae and *Tyrannochthonius beieri*. In the Short Grass the lack of protection from insolation seems to have caused downward movement by the fauna. Depression of vertical distributions here as compared with the Long Grass is seen in 10 out of the 14 groups in Figure 4. The proportions of total individuals extracted from soil and coming from the lower soil samples were: Cover Crop, 24%; Long Grass, 27%; Short Grass, 33%.

Distribution of isotomid species

Four common isotomid species on each site formed a morphosequence of increasing adaptation to life in mineral soil. This involves differences between species in development of the ocelli, pigmentation, length of appendages (Christiansen, 1964), and shape of abdomen: fusiform with tip horizontal in surface and litter species,

TABLE 1. Composition of soil and litter faunas; mean numbers of individuals per sample (275 cm^2); +, taxon present, mean of less than one per sample.

Site	Shifting Cultivation Sequence[1]			Coconut Plantation Transect		Plantation Ground Cover Trial		
Treatment	Forest	Bare Ground	Garden	Zone I	Zone II	Cover Crop	Long Grass	Short Grass
Vegetation structure, rank mass and cover	1	9	6	5 Ib 2	8	3	2	7
Litter layer present (L)	L		L			L		
Depth of soil sampling	0-12.5cm					0-5cm		
Acari	778	363	755	300	144	756	715	708
Collembola, Isotomidae	54	22	37	11	3.2	57	70	73
Other Collembola	110	39	97	76	28	377	196	122
Hymenoptera, Formicidae	53	5.7	22	127	11	192	185	187
Other Hymenoptera	+	-	-	-	-	1.0	+	-
Coleoptera	24	4.1	15	1.3	+	10	9.0	9.0
Diptera (larvae only)	25	3.4	8.6	1.7	+	1.1	+	+
Lepidoptera (larvae only)	15	12	27	2.1	1.4	16.5	+	+
Hemiptera	15	1.2	2.9	3.2	+	23	20	25
Thysanoptera	-	-	-	+	-	-	3.0	6.2
Orthoptera	+	-	-	+	-	+	-	-
Blattodea	1.0	+	+	+	-	+	-	-
Isoptera	+	-	-	-	-	-	-	-
Dermaptera	-	-	-	-	-	-	-	1.0
Diplura	7.0	11	16	+	1.2	4.6	+	1.8
Protura	3.1	2.6	3.5	+	+	8.8	4.2	4.2
Symphyla	19	20	20	26	17	46	26	30
Chilopoda	3.5	-	3.1	2.3	+	7.0	1.2	1.0
Diplopoda	24	2.8	2.0	+	+	36	30	29
Pauropoda	7.0	+	+	5.2	1.7	20	18	43
Pseudoscorpiones	7.1	16	11	1.8	+	+	-	-
Araneida	4.6	1.3	4.6	1.6	1.0	3.2	1.0	+
Opiliones	+	-	1.7	+	+	-	-	-
Palpigradi	3.8	1.4	+	-	-	1.0	1.0	1.2
Uropygi	-	-	+	-	-	-	-	-
Schizomida	-	-	-	+	-	-	-	-
Isopoda	8.4	1.5	+	+	+	+	+	+
Oligochaeta	+	+	+	16	7.5	1.6	+	-
Mollusca	1.0	-	-	+	-	1.4	+	+
Totals	1160	510	1030	577	219	1560	1280	1240

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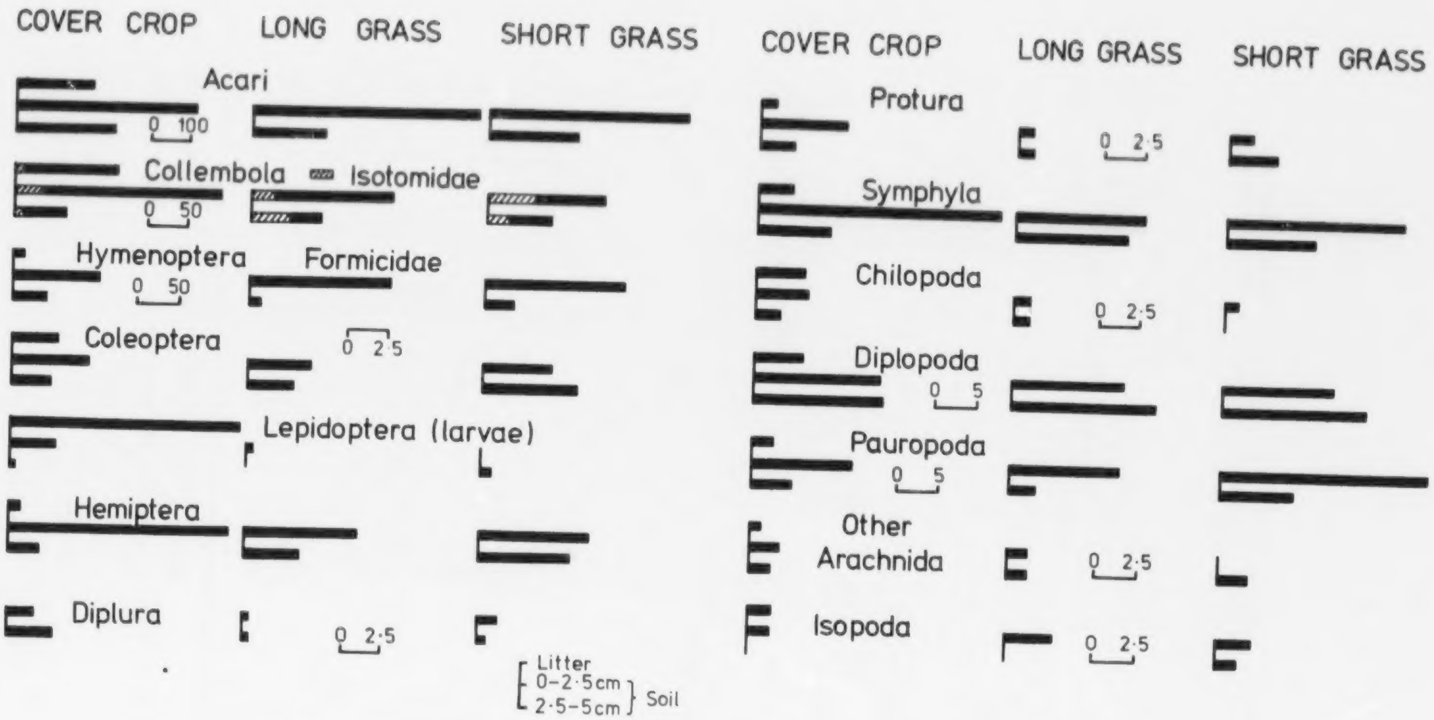

FIGURE 4. Plantation Ground Cover Trial, mean numbers per sample (275cm^2).

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In the Shifting cultivation sequence (Figure 5a), clearing Forest greatly reduced the number of the two species most dependent on a litter layer (compare pseudoscorpions and Diplura, Figure 2). In the single stratum of samples from the Plantation Transect (Figure 5b) the order of increasing penetration of Zone II was the same as the order of penetration of soil in Forest (Figure 5a), a consequence of the surface climate affecting upper profile more than lower profile species (compare Japygidae and Symphyla, Figure 3).

In the Plantation Ground Cover Trial the greatest numbers of Isotomidae came from samples from grasses, the reverse of the treatment distribution of most of the rest of the fauna (Table 1). In the Short Grass, where the rest of the rest of the fauna moved away from the poorly protected soil surface, most Isotomidae came from the upper samples (Figure 5c). As the fauna as a whole returned towards the surface in the Long Grass, most Isotomidae came from the lower samples. This suggests that diffuse interaction with other fauna is an adverse factor operating against Isotomidae at the level of the lower sample in the Short Grass, almost eliminating *Isotomodes*, and at the level of the upper sample in the Long Grass, releasing *Isotomodes*. It is not possible to be more specific as to the nature of the interaction since all the taxa likely to be important as competitors or predators of isotomids had similar vertical distributions (Figure 4).

Composition of isotomid associations

The contributions of each of the four species to total Isotomidae in each treatment are compared in Figure 6. Most tropical forest soils little organic matter (Lee 1969; Burnham 1975). They are not a favourable environment for soil-inhabiting Collembola and in the Forest (Figure 6a) *Isotomodes* was poorly represented. By analogy with the Plantation Ground Cover Trial, the two litter species were adversely affected by interaction with the rich fauna of the litter layer. The long grass of the undisturbed Transect had the most forest-like plantation fauna and its isotomid association resembled that of Forest (Figure 6b), although lower diversity near the surface seems to have allowed an increase in the representation of *C. thermophilus* The immediate effect of clearing Forest on upper profile Isotomidae is shown again in Figure 6c. They may have been barred from the Garden (Figure 6d) by the other two species and the rapid entry of paronellids. The similar combinations of species in Zone II

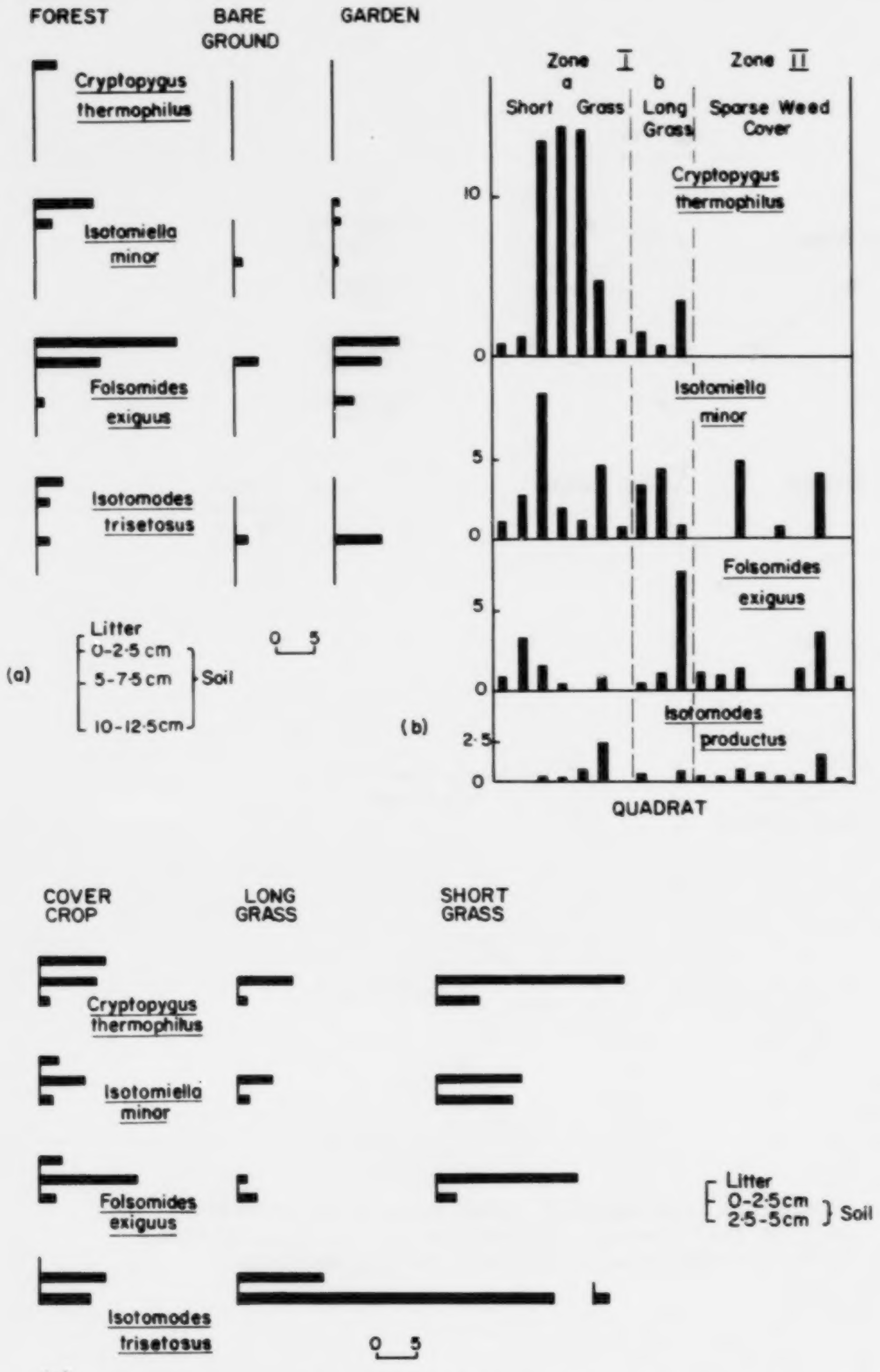

FIGURE 5. Isotomidae (Collembola), mean numbers per sample : (a) Shifting Cultivation Sequence; (b) Coconut Plantation Transect; (c) Plantation Ground Cover Trial.

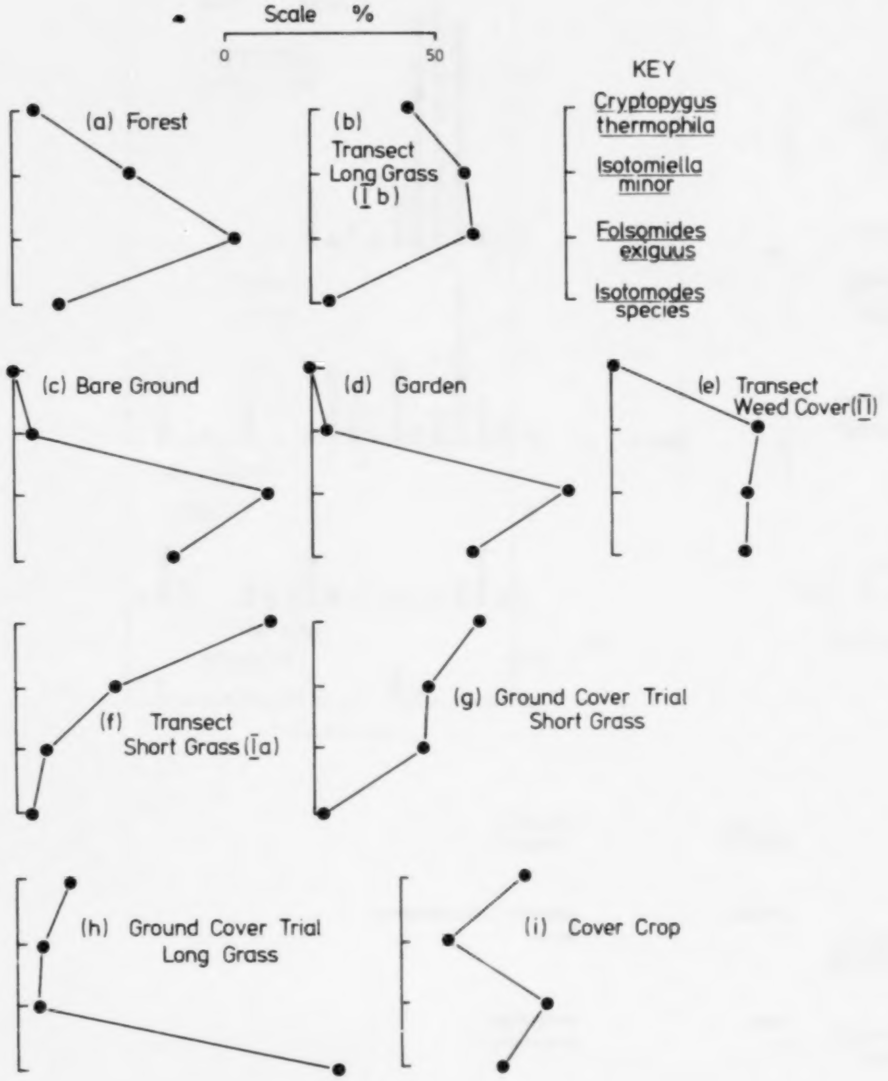

FIGURE 6. Isotomidae (Collembola): total numbers of individuals of each of four species expressed as percentages of total isotomid individuals (see text for explanation).

of the transect (Figure 6e) but with only the uppermost species lacking, can be related to the climate of the soil surface. Under short grass in Zone I of the Transect (Figure 6f) the ant Monomorium talpa appears to have suppressed lower profile Isotomidae as well as mites. The isotomid associations of grasses in the Plantation Ground Cover Trial (Figure 6g,h) were accounted for in the previous section.

The effects of cultivation account for differences in the Isotomidae of the two long grass areas (Figure 6b,h). In Zone Ib of the Transect the fauna was concentrated in a mat of grass litter and roots near the surface. In the Ground Cover Trial, cultivation destroyed this mat and incorporated it into the mineral soil to a depth of ca 5cm, thereby improving the habitat for lower horizon Isotomidae. The balance of species in the Cover Crop (Figure 6i) can be seen as transitional or intermediate between the association in Figure 6h and those in Figures 6a,b.

DISCUSSION

The responses of the soil fauna to disturbance such as cultivation or clearing forest emphasize the importance of the gross morphology of different taxa. This determines species' mode of locomotion on which depends the ability to survive the disturbance by escaping into the soil and the capacity for recolonising by migration. A disturbed fauna's recovery may be slow, limited by rates of recolonisation; the ant communities of these sites take several years to adjust after disturbance, even though the local ant fauna contains many widely distributed, vagile species (Greenslade and Greenslade 1977). Any discrepancy between potential and actual biomass or density of the soil fauna leaves a gap of unused or inefficiently used resources into which opportunist species such as these Isotomidae are likely to expand. Here their occurrence has been explained in terms of two processes, neither of which are sufficient alone: first, there is the action of the same factors that determine the suitability of habitat for other members of the fauna: climate, structure, food supply, effects of ants. Secondly there is diffuse interaction with other soil animals. Whenever the rest of the fauna is poorly developed those isotomid species' different but overlapping habitat requirements allow one or more of them to exploit an opportunity at any level in the upper part of the soil profile. Opportunist behaviour and diffuse interaction are to be suspected whenever a taxon shows ecological release in that its distribution runs counter to the main patterns seen in the rest of the fauna (e.g. Diplura, especially Japygidae, Symphyla, Figures 1-4).

Diffuse competition has been noted also amongst the ants of these sites (Greenslade and Greenslade 1977). If this, or more broadly, diffuse interaction, is frequent in communities of soil animals, quantitative studies of single species in isolation may be misleading. Relationships with a variety of other species could be overlooked. But there are difficulties of sampling, extraction and identification when many species are considered simultaneously. Vlijm Vander kraan and Van Wingerden (1974) recommended quantitative studies of 'Key-species', the most abundant species at each trophic level whose direct functional relationships form a community's 'Skeleton' (Elton 1966). They also refer to Elton's 'Girder system' of indirect relationships involving rarer species. 'Damping down fluctuation and slowing down deviation from the norm.' The process of diffuse competition and the activities of opportunists such as these Isotomidae are part of the girder system. Diffuse competition appears to be one of Elton's (1966)' Strong ecological.......forces against monopoly' (Greenslade and Greenslade, in press).

Anderson and Healey (1972) proposed that fugitive species of Collembola might coexist with superior competitors by moving between temporarily unexploited patches of their habitat, behaviour similar to that described here for opportunist Isotomidae, and by Kaczmarek (1975a,b). To use a single terminology, both opportunist and fugitive species are *r*-strategists in MacArthur and Wilson's (1967) *r* - *K* spectrum (Southwood 1977). The collembolan family Isotomidae contains many species that occur in species-poor communities in disturbed and temporary habitats, on the sea-shore, in deserts, on mountains and in polar regions (e.g. Greenslade and Greenslade, 1973). These environments represent the area in Southwood's (1977, Figures 10,13) 'Habitat templet' of *r*- and Adversity-selection (Greenslade and Greenslade, in press). The species of *Cryptopygus*, *Isotomiella*, *Folsomides* and *Isotomodes* that we discuss here are clearly *r*-strategists apart from the evidence of the present observations. They have efficient dispersal mechanisms and are widely distributed, all being cosmopolitan except for *Folsomides exiguus* which is found throughout Australia, the Pacific and tropical Asia. They are prominent in temporary habitats and may reach high densities there. We see here how *r*-strategists such as these isotomids can also play a part in species-rich, stable, favourable environments. They have the potential to buffer the effects of temporal change in the supply of resources caused by variations in weather or densities of key-species within 'normal' ranges of variation. The populations that expand most rapidly if the availability of a resource increases are those of *r*-selected species and they are most susceptible to the effects of intensified competition as the supply contracts.

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FEEDING BEHAVIOR AND FUNCTIONAL ECOLOGY OF TERMITES OF A TROPICAL SAL FOREST

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INTRODUCTION

Ecological systems must be systematically analized for revealing structure and function of the components in order to have a better understanding and intelligent manipulation of the ecosystem. Ecology of termites has hardly passed the stage of recording facts. The observed facts need a synthesis with a view to test the concepts of ecology. On the basis of monographic studies of all the termite species regarding distribution, biotope niche, diversity and abundance, certain theories may be developed to determine the role of termites in the ecosystems. It is important to determine their function of decomposition of cellulose. as it may effect the soil. Their role in the regeneration of vegetation may be more important than the damage they might cause to agriculture and forestry.

Macfadyen (1963, 1964) constructed a balance sheet for total annual flow of energy through a temperate meadow supporting domestic cattle. Of the total energy captured by plant via photosynthesis, less than 1/7 is respired by the plants, 2/7 is consumed by herbivoures and 4/7 are exploited by "decomposer industry" after the plants have died. There are no comparable figures for tropical grasslands where termites are often very abundant and where they influence the flow of energy at both the herbivore and decomposer level. In such areas the relative respiration of herbivore and decomposers, and thus the fate of plant tissue (primary production) may be strongly influenced by the relative abundance of herbivorous and saprophagous termites.

The most obvious component of a functional niche is nutrition. The food taken from the environment is experimentally defined. Vegetative material contains protein, lipids, nitrogenous bases, and other organic compounds, minerals and water, besides various carbohydrates. The latter constitute 18.7 % by weight of a fresh praire grass (Bouillon 1970). Within the same habitat different species of termites may have a choice of plant species or their special tissues. Beyond the spatial and ecological diversity and decomposition agents which prepare and are a component of diet of many termites. They are present in its general environment, in its nests, and in its digestive tract when different groups of decomposition agents succeed and replace one another. The gradual action of many successive decomposers facilitates to complete the mineralization of plant material.

OBJECTIVES

The goals of this study about two numerically dominant species of termites, Odontotormes obesus Rambur and Odontotermes redemanni Wasmann of a Sal forest at Varanasi, India and to provide quantitative baseline data for compartment modelling in the Indian MAB context to help better understand ecosystem.

Field Activities of Termites Studied

The annual cycle of population, swarming, foraging and construction activities on *Odontotermes obesus* and *O. redomanni* based on the field observations is presented in Figure 1.

METHODOLOGY

Rearing and Maintenance of Termite Population in Laboratory

An incubator was used as an environmental chamber for laboratory rearing. Temperature and humidity within the incubator was controlled at the mound level in complete darkness. The food preference was tested by feeding inside incubator.

Caloric Estimation

The calorie estimation of all the ecological materials was done by Parr Plain Oxygen Bomb Calorimeter (Parr Instrument Company Manual 1968).

Respiration Studies in Laboratory

Respiration measurements were made on individuals of each caste in a Warburg respirameter. The bottom of the respiration chamber had an area of approximately 15 cm$_2$, which is large enough to permit considerable movement of termite (Wiegert 1970).

RESULT AND DISCUSSION

Feeding Habits and Food Preferences

The workers are the only members of the colony which can feed themselves, whereas the other castes are fed by them on the regurgitated and partially digested food. Unlike the finding of Arora and Gilotra (1959), no cannibalism was abserved during this study, in either of the species. The queen was noted to secrete a fatty substance through the pores of her abdomen and the workers were seen licking the sides of her abdomen. Arora and Gilotra (1959) have also reported this behavior. Rajagopal and Veeresh (1976) have studied the food storing habits of *Odontotermes wallonensis* and have reported that they store copped food material from grasses, graminaceous seeds and bark pieces of 1 to 2 mm size in separate cavities which are modified chambers in the middle of the termite mound. But during this study, *O. obesus* and *O. redemanni* both were noted on the semi-decomposed (infected by fungus) moist pieces of non-leaf litter and leaf letter of *Shorea robusta*. When the litter pieces are kept with the fungus garden (fresh) the individuals are noted to prefer the leafy one. None of the test species was observed feeding on the heart wood. Among the leaf litter *O. obesus* was found to prefer the softer part first, while *O. redemanni* took the vein part first. Some blotting paper pieces were also tested for food but none of the species prefered them. Results of of food preference tests are given in Table 1.

Figure 1. A COMMON GRAPHIC REPRESENTATION OF ANNUAL CYCLE OF POPULATION, SWARMING, FORAGING AND CONSTRUCTION ACTIVITIES IN *Odontotermes obesus* Rambur and *O. redemanni* Wasmann (Based on field observations).

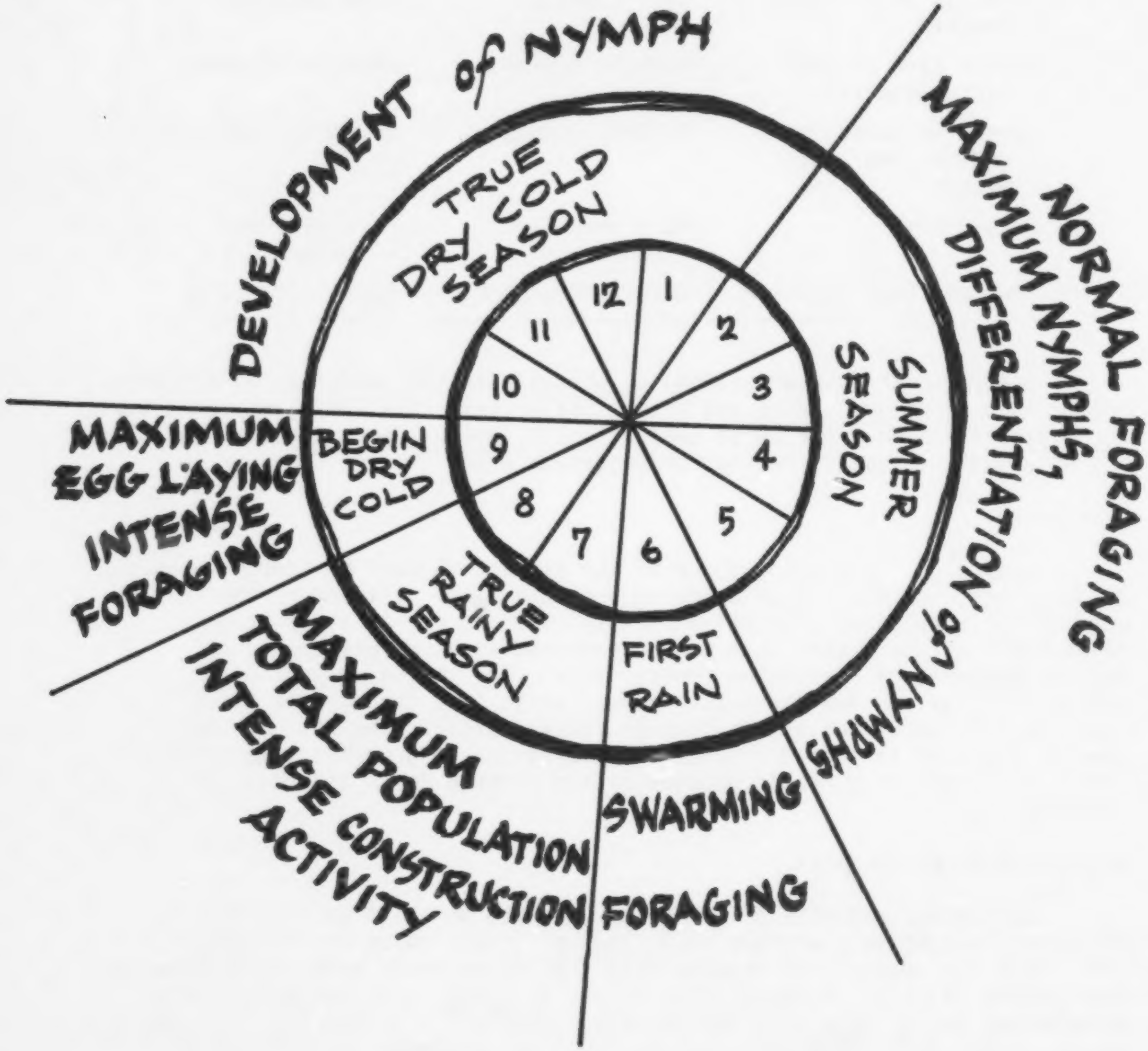
DEVELOPMENT of NYMPH
TRUE DRY COLD SEASON
12
1
2
3
4
5
6
7
8
9
10
11
SUMMER SEASON
NORMAL FORAGING
MAXIMUM NYMPHS, DIFFERENTIATION of NYMPHS
MAXIMUM EGG LAYING
INTENSE FORAGING
BEGIN DRY COLD
TRUE RAINY SEASON
FIRST RAIN
MAXIMUM TOTAL POPULATION
INTENSE CONSTRUCTION ACTIVITY
SWARMING
FORAGING

Table 1: FOOD PREFERENCES OF ODONTOTERMES OBESUS AND O. REDEMANNI

FOOD	DEGREE OF CONSUMPTION	
	O. obesus	O. redemanni
Heart wood of sal	Not consumed	Not consumed
Fresh bark (living)	Not consumed	Not consumed
Dry moist dead bark	Consumed	Consumed
Veins of leaf litter (moist)	Less consumed	More consumed
Softer part of leaf litter (moist)	Heavily consumed	Heavily consumed
Fungal infected leaf and non-leaf moist litter	Severely consumed	Severely consumed
Fungus comb	More severely consumed	More severely consumed
Cow dung (not fresh)	Heavily consumed	Heavily consumed

According to Kushwaha (1964) O. obesus eats the seedlings of different plants like Mangifera indica and Citrus while Chatterjee (1970) reported that Eucalyptus is perhaps the worst sufferer of O. obesus feed. Agarwal (1970) has observed the species feeding on sugarcane also.

Energetics

Energy is the driving force of the system. A part of energy exposed to decomposer system, (input to decomposer cycle) is utilized by the termite population. The major proportion of this utilized energy is spent on the maintenance of population that can be referred to as maintenance cost. This is measured by respiratory energy loss. The remaining part of the utilized energy has two channels. A part of it goes through the first channel, the decomposer system through faecal matter. The rest of the energy is stored in second channel in form of tissue growth. Some of the energy also goes into the decomposer system through death and decay of individuals.

Energy Intake by Termites

Laboratory colonies of O. obesus consumed more litter than 8% of their body weight/day, whereas in O. redemanni this value reaches about 10%. Both the species can consume more than 9% of their oven dry body weight/day (Tables 2A, B). In terms of calories, O. obesus consumed 352.2 cal/g termite/day and O. redemanni 404.34 cal/g termite/day (Table 2A). Of the amount eaten, 51% (181.6 cal/g termite/day) in O. obesus and 41% (165.6 cal/g termite/day) in O. redemanni are assimilated. Seifert (1962) found that in feeding experiments, Kalotermes flavicollis, with a mean weight of

Table 2A CALORIC INGESTION, ASSIMILATION AND EGESTION OF LITTER BY TERMITES (CAL/G TERMITE/DAY)

SPECIES	CONSUMPTION (C)	ASSIMILATION (A)	EGESTION (C-A)
Odontotermes obesus	356.20	181.56	174.6
O. redemanni	404.34	165.65	238.7

Table 2B FOOD (DRY LEAF & NON-LEAF LITTER) CONSUMPTION, EGESTION AND ASSIMILATION BY TERMITE (MG/G TERMITE/DAY)

SPECIES	CONSUMPTION	EGESTION	ASSIMILATION	ASSIMILATION EFFICIENCY (%)
O. obesus	87.3	42.8	44.5	51
O. redemanni	99.1	58.1	40.6	41
Mean	93.2	50.6	42.6	46

about 7/mg/animal, ate 0.16 - 0.18 mg of pine sap and heart-wood per day, i.e., 2-3% of fresh body weight. More than 60% of the amount eaten was completely assimilated (0.098 - 0.11 mg/termite/day or 13.0 to 15.7 mg/g termite/day). The rates of food consumption of Nasutitermes exitiosus, measured by Lee and Wood (1971), are less than half that measured by Siefert (1962) in K. flaivollis. In both the cases, cultures were maintained at 26°C, but the different termite species used may have affected the results. The food material tested was different, and the culture methods used by Siefert differed in many respects from that of Lee and Wood (1971). The assimilation rates measured in my present study are nearer to those of Lee and Wood (1971) who reported it to be 54%. But it is lower than that of K. flavicollis as recorded by Seifert (1962).

The mean energy intake by total termite population in the study area is more than 34 cal/m^2/day which comprises about 19 cal of energy consumed by O. redemanni and 16 cal by O. obesus populations /m^2/da (Table 3). Egested energy was calculated by subtracting the percentage of assimilation (51% O. obesus and 41% O. redemanni) from ingested energy values. Because of the higher assimilation efficiency of O. obesus than that of O. redemanni the calculated egested energy of O. redemanni (11/1 cal/m^2/day) is more than that of O. obesus (7.85 cal/m^2/day). In contrast, O. redemanni (7.7 cal/m^2/day) could assimilate less energy than that by O. obesus (8.13 cal/m^2/day).

Table 3 - Intake egestion and assimilation of energy by termites in Varanasi forest (cal/m^2/day)

Month	*Odontotermes obesus*			*O. redemanni*			Total on area basis		
	Intake	Egetion	Assimilation	Intake	Egetion	Assimilation	Intake	Egetion	Assimilation
1975									
January	12.7549	6.2521	6.4813	14.6982	8.6770	6.0215	27.4531	14.9291	12.5028
February	9.5888	4.7002	4.8725	17.0124	10.0432	6.9696	26.6012	14.7435	14.9157
March	8.5654	4.1985	4.3524	11.4804	6.7831	4.7072	20.0462	9.5117	9.0596
April	6.7787	3.3220	3.4445	8.9927	5.3132	3.6872	15.7714	8.6352	7.1317
May	9.6051	4.7082	4.8807	11.3470	6.7042	4.7042	4.6525	20.9521	11.4124
June	21.6821	10.6280	11.0176	24.0720	14.5844	9.8701	45.7541	25.2124	20.8377
July	36.4845	17.8837	18.5393	38.5023	22.7487	15.7868	74.9867	40.6324	34.3261
August	26.3689	13.3991	27.8012	16.4260	11.4260	11.3991	54.1701	29.8591	24.7982
September	25.6291	12.5627	13.0232	31.3370	18.5152	12.8489	56.6291	31.0779	25.8721
October	11.8148	5.7913	6.0036	13.3495	7.8874	5.4736	25.1643	13.6787	11.4772
November	11.8076	5.7878	5.9999	14.4377	8.5303	5.9198	26.2453	14.3181	11.4772
December	10.9858	5.3849	5.5823	13.4897	7.9703	5.5311	24.4755	13.3552	13.5526
Mean	16.0055	7.8454	8.1330	18.7734	11.0921	7.6998	34.7790	18.9470	15.8320

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Respiratory Energy Loss

The values of oxygen consumption measured by Warburg's apparatus in laboratory are converted to caloric equivalents and used to calculate the respiratory energy loss of the termite population both on per mound and per meter square basis (Table 4). This conversion is made on the assumption that the combustion of 1 litre of O_2 (STP) produces 4.7 K cal biomass (Brody, 1945 and Lee & Wood, 1971). It is evident from Table 4 that the individual energy consumption of workers (0.201 cal/day) and nympns (0.073 cal/day) of *O. redemanni* is more than that of *O. obesus* (0.196 cal/day worker and 0.055 cal/day nymphs). The erverse is the case with imago (1.21 cal/animal/day *O. obesus* and 0.884 cal/animal/day *O. redemanni*) and soldier (*O. obesus* 0.22 cal/animal/day and *O. redemanni* 0.165 cal/animal/day). In a total computed respiratory energy loss of 14.315 cal/m^2/day, *O. redemanni* (7.365 cal/m^2/day) loses slightly more than O. obesus (6.95 cal/m^2/day) does.

Oxygen consumption values from this study in relation to body weight agree with the values given by Wiegert (1965) and Smalley (1960) for several species of grasshoppers and Wiegert (1970) for termite (*Nasutitermes costalis*). Golley and Gentry (1964) found the oxygen consumption of ants of genus *Pogomyrmex* to be on order of 8-10 times greater than that of grasshoppers studied by Wiegert or Smalley. Thus it can be admitted that the termites are rather sedentary animals compared to most ants; yet they did not exhibit a moderate amount of activity in the respirometers i.e., they are more active in nature. Furthermore, this low rate of oxygen consumption cannot be due entirely to lowered activity levels because sedentary meadow spittlebug nymphs as reported by Wiegert (1964) had normal rate of oxygen consumption.

Respiratory CO_2 release of an entire population in nature was measured directly by alkali absorption method. These values were converted at STP and their caloric equivalent has been computed. Assuming a value of 6.0 cal/ml CO_2 with non-protein R.Q. of 0.80, the data are tabulated in Table 5. It is evident from this table that the respiratory energy loss per m^2 from *O. obesus* (15.24 cal/day) population is higher than that of *O. redemanni* (12.97 cal/day). The ratio of respiration estimated by the traditional Warburg laboratory method (14.315 cal/m^2/day) to population respiration measured by alkali absorption method (29.18 cal/m^2/day) is 0.496. The data of respiratory energy loss measured under field conditions are more than double as obtained by Warburg method presumably because it also includes the respiration of termitophilas, bacteria and fungi. The animals do not remain as active in the Warburg apparatus as in the field. Secondly, the respiratory energy loss by eggs has not been included in the laboratory method which also adds to the lowering of the total respiratory energy loss by traditional Warburg apparatus method. Odum *et al.* (1962) and Wiegert (1965) have also found the laboratory method to be underestimating. Wiegert (1970) has also reported notable difference of respiratory activity as measured in field and laboratory. It may be noted that he used infra-red gas analyser instead of alkali absorption for estimating CO_2 output. The real value of respiratory energy loss of population lies somewhere between 14.315 cal/m^2/day and 29.180 cal/m^2/day.

Table 4 - RESPIRATORY ENERGY LOSS OF TERMITES (O. obesus and O. redemanni) IN LABORATORY CONDITIONS AT NAUGARH FOREST - VARANASI (CALCULATED ON BASIS THAT THE COMBUSTION OF 1 LITRE OF O_2 PRODUCES 4.7 K CAL BIOMASS - LEE AND WOOD, 1971)

CATEGORY	Odontotermes obesus			O. redemanni			Total (O. obesus and O. redemanni)		
	Per Individual Day	$Mound^{-1}$/ Day	m^{-2}/day	Per Individual Day	Per Mound Day	m^{-2}/day	Per Individual Day	Per Mound Day	m^{-2}/day
WORKER	0.196	10670.60	5.29	.201	15000.0	5.9	.397	25670.5	11.315
SOLDIER	0.220	645.04	0.33	.165	632.3	0.3	.385	1277.3	0.576
NYMPH	0.055	574.37	0.29	.073	1135.2	0.5	.128	1709.4	0.740
IMAGO	1.210	1867.03	0.94	.89	1871.4	0.7	2.84	3738.5	1.684
Total	--	13756.68	6.950	--	18639.1	7.4	--	32395.8	14.315

All values are in calories

Energy Flow

The food energy metabolized by an animal is ultimately utilized in the performance of several basic organismic functions. As a result, the total energy budget can be partitioned between the requirements of basal metabolism (respiratory energy loss at rest) activity expenditure and production of biomass. Presumably a small fraction of respiratory energy is lost due to calorigenic effect (increase in heat production following food consumption when the animal is in a thermo-neutral environment).

Thus the total energy requirement of an animal population can be represented by the equation:

$$I = R + P + E$$

where,

I = Ingestion of total energy intake
R = Energy loss at heat
P = Net increase in energy content
E = Energy content of food material egested or eliminated from the body

The flow component is therefore sum of R + P.

The total annual secondary production of 412.5 cal/m^2/yr (210.95 cal/m^2/yr, O. obesus and 202.3 cal/m^2/yr O. redemanni) is about 7.32% (3.74% O. obesus and 3.59% O. redemanni)of the total energy flow (Table 5), through termite population in the area. But the production of O. obesus and O. redemanni are equivalent to about 7.68% and 7.99%, respectively, of the annual energy flow through the population of respective species.

The compartmental flow of energy through termite population at Varanasi forest is shown in Figure 2.

Maldague (1964), Wiegert (1970) and Hebrant (1970) have estimated populations and energy flow of termites in tropical rain forests and savanna in Central America and West Africa. These results have been compared with those of the present study (Table 6). Wiegert's estimates show that termites utilize 0.26% of total available energy which differ little from my data. While according to Maldague's population estimates, the termite would utilize about 2.53% of the available food energy. Although the population /m^2 in Puerto Rico (120/m^2) is more than one and a half times higher than that of Varanasi forest (74/m^2), the total energy flow of both the studies are more or less similar. In the present study both the test species have nearly equal share of total energy flow/m^2/yr. The total energy flow estimated by Hebrant (1970) was about three times (14 K cal/m^2/yr) more than that reported herein (5.637 K cal/m^2/yr). Thus the mound building termites in the Varanasi forest, with a total energy flow of about 6 K cal/m^2/year seem to represent only a small fraction of the total input of energy into the detritus decomposers food chains.

Table 5 - CO_2 evolution and respiratory energy loss from termite population at study site infield conditions (energy loss has been calculated as described by Wiegert, 1970 - 6 cal/ml CO_2)

Month	CO_2 evolution/mound		Respiratory energy loss cal/day				
			Per mound		Per meter square		
	O. obesus (ml/day)	O. redemanni (ml/day)	O. obesus	O. redemanni	O. obesus	O. redemanni	Total
1975							
January	4354	5053	26124	30318	13.192	11.975	25.167
February	4201	5256	25206	31536	12.729	12.456	25.185
March	4106	4205	24636	25230	12.441	9.965	22.406
April	3505	4075	21030	24450	10.620	9.682	20.302
May	4515	4384	27090	26304	13.680	10.416	24.096
June	5753	6105	34518	36630	17.431	14.468	31.899
July	6803	8254	40818	49524	20.613	19.561	40.174
August	7004	8053	42024	48318	21.222	19.085	40.307
September	6751	9154	40506	54924	20.455	21.694	42.149
October	4655	4955	27930	27930	14.104	11.654	25.758
November	4302	5603	25812	33618	13.035	13.280	26.314
December	4405	5501	26430	33006	13.347	13.370	26.384
Average	5029.5	5883.2	30177	35299	15.240	12.970	29.180

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Figure 2. FLOW OF ENERGY THROUGH TERMITE POPULATION IN VARANASI FOREST

P - Primary Producer compartment
S - Secondary Producer compartment
D - Decomposer compartment

All values are in K. calories; Values on arrows are rates of flow ($/m^2/da$)

NPP - Approximate net primary productivity $/m^2/yr$
NAD - Net imput to decomposer cycle $/m^2/yr$ per mwtwr square/yr.
SCT - standing crop of termite $/m^2$
TU - termite utilization $/m^2/yr$
TP - termite production $/m^2/yr$
R - Respiratory energy loss $/m^2/yr$
E - Egested energy $/m^2/yr$

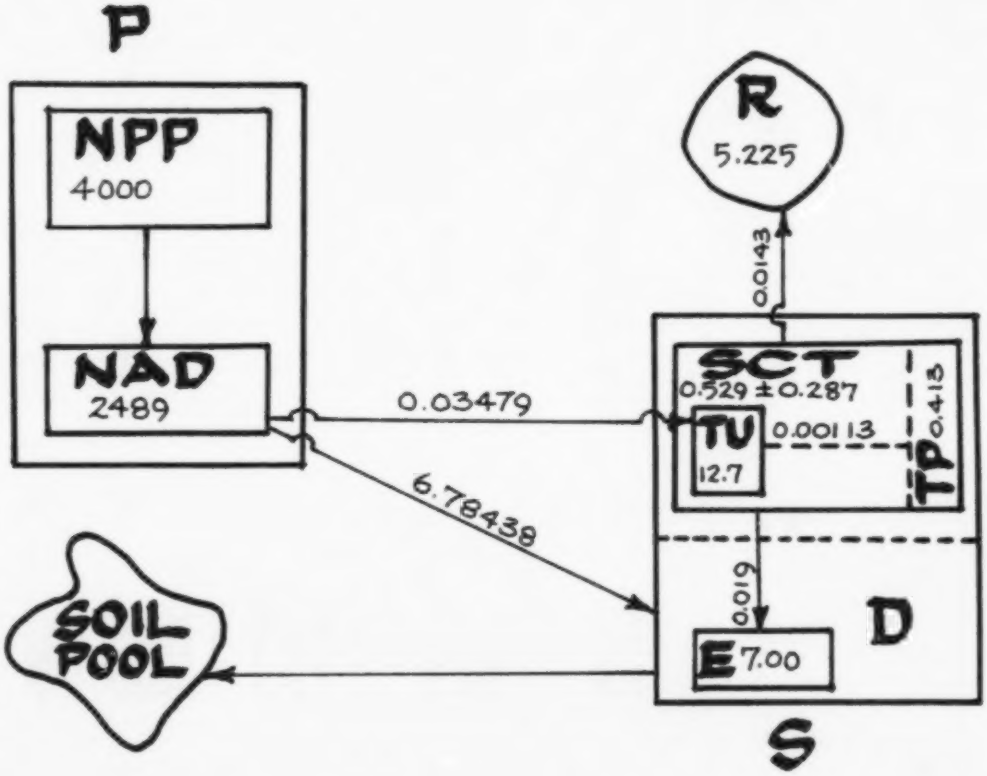
P
NPP
4000
NAD
2489
0.03479
6.78438
R
5.225
0.0143
SCT
0.529 ± 0.287
TU
12.7
0.00113
TP
0.413
0.019
D
E 7.00
SOIL POOL
S

Table 6 - ENERGY CONSUMPTION BY TERMITES IN TROPICAL FOREST AND SAVANNA

VEGETATION	TERMITES								
			BIOMASS						
	Species	NO m^{-2}	g/m^{-2}	K cal/ m^2/yr	Total Energy Flow K cal/ m^2/yr	Productive on K cal/ m^2/yr	Total Available Energy K cal/m^2/ year	% Energy Utilized by Termite	References
Rain forest (Yangambi, Congo)	Various Species	-	11.0	-	133.9*	-	5290	2.53	Maldague (1964)
Rain forest (El Verde, Puerto Rico)	Nasutitermes costalis	120	0.075	0.599	5.86	0.474	2255	0.26	Wiegert (1970)
Savanna (Congo)	Cubitermes exiguus	-	1.15	-	14.00	0.90	-	-	Hebrant (1970)
Deciduous Forest dominated by Sal Varanas, India	Odontotermes obesus	36	0.045	0.259	2.747	0.2109	2489	0.1104	Present Study
	O. redemanni	38	0.046	0.270	2.891	0.2023	2489	0.1161	
	O. obesus + O. redemanni	74	0.092	0.529	5.637	0.4125	2489	0.2265	

* Calculated energy utilization estimates of Hebrant (1970) for Cubitermes exiguus

ACKNOWLEDGMENT

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SESSION VIII: BASIC SOIL ECOLOGY: NUTRIENT CYCLING, MICROORGANISM-FAUNAL RELATIONSHIPS, FEEDING AND REPRODUCTIVE STRATEGIES

Moderator: Stuart B. Hill

Macdonald College of McGill University
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THE FATE OF CATIONS IN BEECH AND SPRUCE LITTERS INCUBATED *in situ*

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INTRODUCTION

The aim of the research is to assess the impact of Spruce forests upon the environment and specially upon the nutrient budget compared with the caduceous forests.

For this purpose, it was decided, in a first step, to study from a dynamic point of view the leaching rate of cations from litter falls in a Beech forest and a Spruce forest. These forests are located in the "Hautes Ardennes" district, in Belgium, (Altitude 555 meters) on acid brown soils.

METHODS AND MATERIALS

The cation evolution was recorded for 27 months in Beech leaves and Spruce needles in order to know the long term behaviour of decomposing litters. Beech leaves and Spruce needles were sampled in Autumn 1976, air-dried for 3 weeks to a constant weight after the method of Lousier and Parkinson (1976). Subsamples were oven-dried at 85° C with a view to determining the correction for dry weight.

Ten grams litter were put in a (1 x 2) mm mesh net rectangular plastic bag (20 cm x 20 cm x 5 cm in size). So, ten grams litter covered 400 cm^2 which was similar to the annual litterfall (Lousier and Parkinson, 1976). The (1 x 2) mm mesh net was chosen to minimize leaf drop-out and to avoid water immobilization in the bag.

Sixty bags were made up respectively for Beech leaves and for Spruce needles. The bags were placed on the soil surface.

At each sampling time (ca every month), 3 to 5 bags were taken at random and analyzed for K, Na, Ca, Mg, Fe and Pb by atomic spectrometry. Besides, a faster method was applied in order to assess the release of metal ions. It was similar to the Nilsson method (Nilsson, 1972). On the basis of the decomposition degree and morphological features, the Beech leaves were divided into four different classes and the Spruce needles into three different classes. By this way, each class contains leaves or needles decomposed to a defined degree. After drying, 100 leaves or needles from each class were counted and weighted separately in order to obtain the mean weight. Therefore, it was possible to evaluate the mean amount of elements per leaf or per needle.

Besides, leaf falls were recorded in the Beech and Spruce forests in order to know the cation pool per surface unit : they averaged 2908-2836 and 1650 Kg/ha respectively in Beech forest and Spruce forest.

RESULTS

First, we have evaluated the total input of nutrients by litterfall in both forests by knowing the litterfall amounts and the cation concentration. We have compared our results with the data of similar French forests (Table 1).

TABLE 1. Input of cations by litter fall (Kg/Ha) in Beech (B) and Spruce (S) forests.

	K		Mg		Fe		Ca	
	B	S	B	S	B	S	B	S
Parmentier (1976), Belgium	5.4	2.9	1.4	0.6	0.85	0.78	20	6.5
Aussenac *et al* (1969), France	5.6	2.4	1	0.7	0.4	0.4	14.5	11

It will be seen that the amounts of cations in the French and Belgian forests are similar and that the inputs are always lower in Spruce forests than in Beech forests. Now, let us examine the cations evolution during the Beech leaves decomposition in plastic nets. The units expressing the cation content were very important. Indeed, owing to the decomposition, the weight of leaves decreased more or less rapidly. This fact caused an obvious weight difference specially between the three years old leaves and the just fallen leaves. This loss of organic matter conduced to a relative increase in element concentration (Remacle and Vanderhoven, 1973). But this relative increase is eliminated by calculating the cation content as mg/leaf (or needle) and g/m^2. We have adopted these units. The results are summarized in Table 2. In this table, all the cation contents are related to the same initial basis, index 100 in December, in order to compare the evolution of the different cation amounts vs time easily.

TABLE 2. Weight and cation contents in Beech leaves. December : index 100.

		Leaf weight	K	Na	Ca	Mg	Fe	Pb
1976	December	100	100	100	100	100	100	100
1977	January	82	41	55	76	60	113	164
	February	81	30	42	75	71	136	127
	May	78	37	41	63	54	168	-
	June	77	34	34	56	56	179	176
	Augustus	72	39	24	56	54	179	87
	September	70	30	21	48	57	233	115
1979	March	66	35	39	41	52	413	279
	September	65	23	38	38	27	413	-
	October	64	28	24	32	42	388	411
	November	64	28	56	33	26	458	-
1979	March	60	17	-	35	32	501	386

It appears that the most important leaching process occurs just after the beginning of the experiment i.e. after the litter-fall and during the greatest loss of the litter weight. So, 59 % Potassium are leached during the first month, it means that 3.2 Kg K/ha are supplied to the bottom horizons. Further losses are then very low. The one-year-old leaves still contain 1.6 Kg K/ha, then after two years' incubation, 78 % are released only.

Similar trends are observed for Sodium, Calcium and Magnesium contents. However, the decrease of Calcium and Magnesium contents is slower than for Potassium and Sodium and closer to the weight loss of litter.

On the contrary, Iron and Lead tend to accumulate during litter decomposition. The Iron and Lead contents are respectively four times and seven times as high as the initial contents.

Therefore, by considering the cation losses vs litter decomposition, it is possible to identify three types of ion evolution :

- The first group is mainly represented by Potassium and Sodium evolution, the ions disappear much faster and more rapidly than the decrease of organic matter; this is obvious in the first months of incubation.
- In the second group, the release of the nutrients Calcium and Magnesium is slower. The release of Calcium is rather similar to the organic matter decrease.
- Finally, Iron and Lead belong to the third group, in which the contents increase with decomposition

As to the Spruce needles decomposition and cation contents, the evolution of needle weights was difficult to assess as owing to their thin shape, some needles escaped out the plastic net making evaluation of weight decrease and ion content a difficult task.

However, by considering the ion concentrations the same groups of evolution can be recognized as in beech litters (Table 3).

TABLE 3. Cation concentrations in incubated litters, B : Beech leaves, S : Spruce needles (December : 100)

	K		Na		Ca		Mg		Fe		Pb	
	B	S	B	S	B	S	B	S	B	S	B	S
1976 Dec.	100	100	100	100	100	100	100	100	100	100	100	100
1977 Jan.	50	39	67	73	93	90	73	75	138	94	200	122
Feb.	37	30	52	68	93	83	88	68	168	102	157	146
May	48	35	52	59	81	63	69	75	215	132	-	171
Jun.	44	35	44	64	73	57	73	73	232	132	229	185
Aug.	54	31	33	64	78	51	75	60	249	153	121	263
Sep.	43	31	30	68	69	58	81	55	333	140	164	293
1978 Mar.	53	30	59	77	62	71	78	63	626	202	414	341
Sep.	35	32	59	64	57	-	41	60	626	334	-	488
Oct.	43	34	37	68	50	53	65	73	606	449	642	463
Nov.	44	30	88	77	51	42	41	78	716	426	-	-
1979 Mar.	29	27	-	-	59	53	53	55	835	474	644	463

Concerning Potassium, it can be assumed that 2 Kg K/ha are lost during the first month of incubation, which is lower than in beech litter.

Besides, the ion evolutions were evaluated by the Nilsson method.Beech leaves litters and Spruce needles litters were sampled from the soil surface and divided respectively into four and three fractions in relation to their degree of decomposition (Table 4).

TABLE 4. Cation content in Beech leaves and Spruce needles.

a) Beech leaves classes (class 1 : Index 100).

Class	Weight	K	Na	Ca	Mg	Fe	Pb
1	100	100	100	100	100	100	100
2	88	22	27	75	68	90	-
3	57	7	18	48	46	70	83
4	37	9	12	32	30	100	116

b) Spruce needles classes (class 1 : Index 100)

Class	Weight	K	Na	Ca	Mg	Fe	Pb
1	100	100	100	100	100	100	100
2	105	28	14	90	52	100	115
3	71	20	9	31	33	120	149

Again three groups can be distinguished in Beech litters as well as in Spruce litters.

- The group characterized by Sodium and Potassium, in which the nutrient release is faster than the leaf weight loss. For example, whereas the decrease of litter weight equals 43 %, the release of Sodium reaches 92 %.

- The group characterized by Ca and Mg. In these cases, the release of the nutrient is well correlated with the decrease of leaf weight mainly in the case of Beech litter.

- Finally, the accumulation of Iron and Lead.

We plan, in further observations, to divide the leaves and needles in a greater number of fractions in order to obtain more accurate data about the ion evolution. Nilsson (1972), Denayer-de Smet (1974) and Mignolet (1977) also noted Lead accumulation in litters. Nilsson assumed that this accumulation resulted from a positive sorption process connected with the leaching from the tree canopies and aerosol or metal ions deposits, Lead being stored in leaf canopy through root absorption as expected by Denayer-de Smet (1974). Besides, an upwards flux of cation cannot be excluded. The Lead storage may delay the litter decomposition. The same processes can be implicated in the Iron accumulation (Gosz *et al.*, 1973, Lousier and Parkinson, 1978). This Iron accumulation could influence the Nitrogen cycle. Indeed, it could lead to an immobilization of nitrate ions by adsorption on anion exchange sites provided by iron oxides (Vitousek *et al.*, 1979). Finally, it must be noted that the release of cations from litters is complicated by the fact that the inputs of cations due to rain and through fall can be very important and much higher than the cation contents of leaves and needles. For example, 31 Kg K/ha.year are supplied by canopy leaching under Beech forest i.e. six times the leaves fall input; under Spruce forest, 17 Kg K/ha year are contained in canopy leaching, which equals also six times the Potassium input by needles fall.

CONCLUSIONS

From these preliminary data, it can be concluded

- The inputs of the nutrients K, Na, Ca, Mg are higher under Beech forests than under Spruce forests. This is true for litter fall and canopy leaching.

- These nutrients are released from the litters mainly at the beginning of the decomposition.

- The fate of nutrient in leaves and needles litter can be characterized by three types of evolution,

  - a leaching rate greater than the decomposition rate
  - a leaching rate more or less correlated with decomposition

- an accumulation of ion during decomposition.

- The supply of nutrients by rain and canopy leaching is more important than the release by litter.

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QUESTIONS and COMMENTS

M.S. GHILAROV: Were there animals inside net bags? Was the increase of lead and iron in percents to dry weight or in absolute values?

J. REMACLE: The leaves and the needles are air-dried before being arranged in the net bags. Therefore it can be assumed that animals can be killed. The increase of lead and iron are expressed in absolute values (mg/leaf or needle or mg/m^2).

ANNUAL CARBON, NITROGEN, AND CALCIUM TRENDS IN LITTER AND SURFACE SOIL OF A MIXED HARDWOOD STAND

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INTRODUCTION

A large body of literature has been generated, in recent years, on nutrient cycling in forest ecosystems (Gosz et al., 1973; MacLean and Wein, 1978; Lousier and Parkinson, 1978; Pomeroy, 1970). Most of this information is concerned with litter decomposition and primary productivity. While this is important information, one area often neglected is the nutrient relationships between the litter layer and the soil.

The nutrient dynamics of forest litter is often monitored using litter bags. This is an ingenious method of analyzing the decomposition of a known quantity of litter, but the technique does have its drawbacks. First, there is the problem of mesh size. With small mesh sizes, invertebrates are excluded, and with large mesh sizes fragments of the litter are often lost. The other serious problem associated with litter bags is that usually the moisture regime of the litter in the bags is higher than the surrounding litter. Finally, the mirgation of the litter bags down through the litter layers is often at a different rate than unconfined litter.

The purpose of this research was 1) to analyze the carbon, nitrogen, and calcium trends in unconfined mixed hardwood litter concurrent with weight loss for one year, 2) to determine the elemental trends of the surface soil and relate their nutrient fluxes with litter trends from the same sites, and 3) to suggest differences between earlier litter bag-nutrient studies with those of unconfined litter. Correlation and partial correlation techniques were used to investigate the various trends.

METHODS

RESEARCH SITE

A 50 x 50 m area was staked out and subdivided into 10 x 10 m quadrats in a mixed hardwood site. Samples were collected in the first week of every other month for one year, starting in February 1977. The February samples were collected from under about 70 cm of snow, and the following December samples were collected from under about 10 cm of snow.

Five 10 x 10 m plots were selected for each sampling period. From each plot, two litter samples (730 cm^2 each) and two soil samples

(5 cm diameter x 10 cm deep) were collected. No distinctions of F, L, and H layers were possible because virtually all leaf litter disappeared from the soil surface by fall.

LITTER SAMPLE ANALYSIS

The litter was handsorted for macro-invertebrates, then oven dryed at 60°C for 72 hours and ground in a Wiley mill to pass a No. 20 mesh (840 μ) screen. Carbon was determined by a modification of the colorimetric technique presented by DeBolt (1974). Kjeldahl digestion procedures and an ammonium specific ion probe method, as described by Bremmer and Tabatabai (1972) and Nelson and Sommers (1972) were used for nitrogen. Calcium determinations were made with a calcium ion probe after dry ashing, as described by Allen et al. (1968). Litter weight was determined to two decimal places. All litter analyses were run in duplicate.

SOIL SAMPLE ANALYSIS

The soil samples were air dryed and sieved to pass a 4 mm mesh screen. Carbon and nitrogen levels were determined with the above technique. Exchangeable calcium determinations were made with a specific ion probe after extraction with soidum acetate (Woolsen et al., 1979). Determinations of pH were made with a Fisher calomel electrode. All soil analyses were run in quadruplicate.

RESULTS AND DISCUSSION

LITTER SAMPLE WEIGHT (Figure 1)

The first point of interest in the litter sample weight graph is the low average sample weight in December relative to the previous February. Litter fall commenced both years around the second week of October. In the fall previous to sampling, cold weather and accumulated snow reduced the rate of removal of fresh litter by invertebrates. The following fall was unseasonably warm. Consequently, the invertebrate populations were more active, and a substantial amount of the fresh litter was decomposed and comminuted before snow accumulation.

The weight loss in litter bag studies often follows a negative exponential curve. Justification for this relationship was developed primarily by Olson (1963). Using litter bags Minderman (1968) found that a good negative exponential curve fit could only be obtained with a homogenous litter source. When several types of litter are mixed, the negative exponential equation is no longer valid. We regressed our data from this study using both a negative exponential model, and a linear model. There was no difference between the r square values. This suggests that our system with 11 tree species and using leaf as well as woody branch litter in our samples has too many litter components with different decomposition rates to fit a negative exponential model. Therefore, we conclude that the reduction of weight through time, in our system is best represented with a linear model.

CHARACTERISTICS of MIXED HARDWOOD FOREST LITTER

SUNY LAFAYETTE EXPERIMENTAL STATION · SOIL ECOLOGY LABORATORY · ONONDAGA CO., NY

FIGURE 1

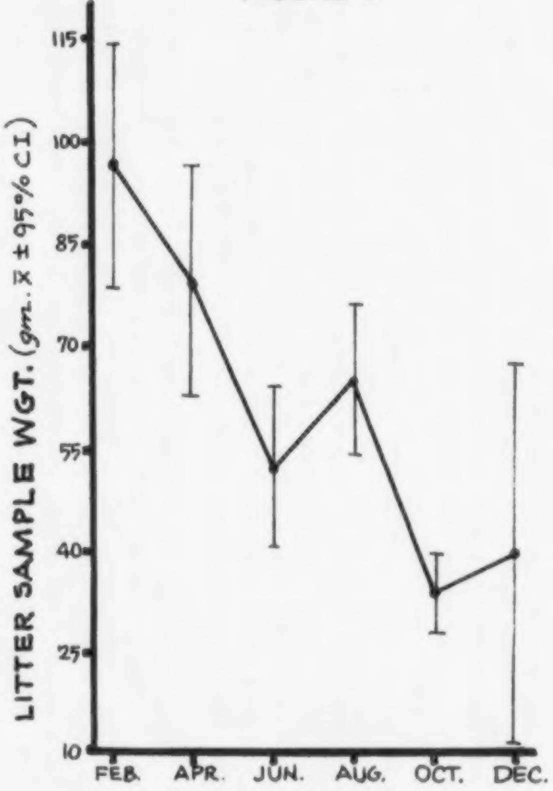


FIGURE 2

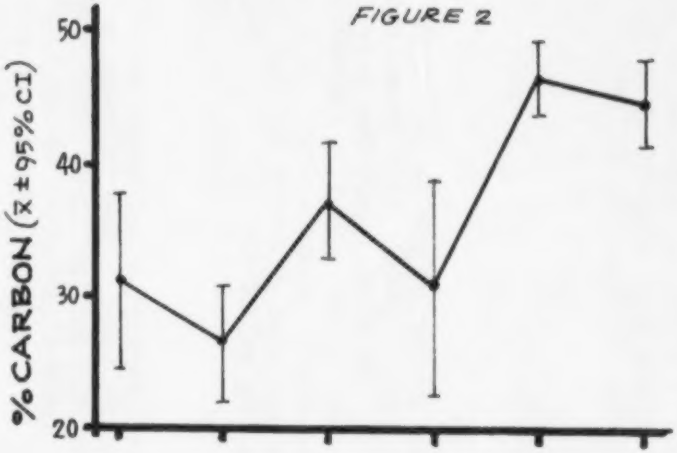
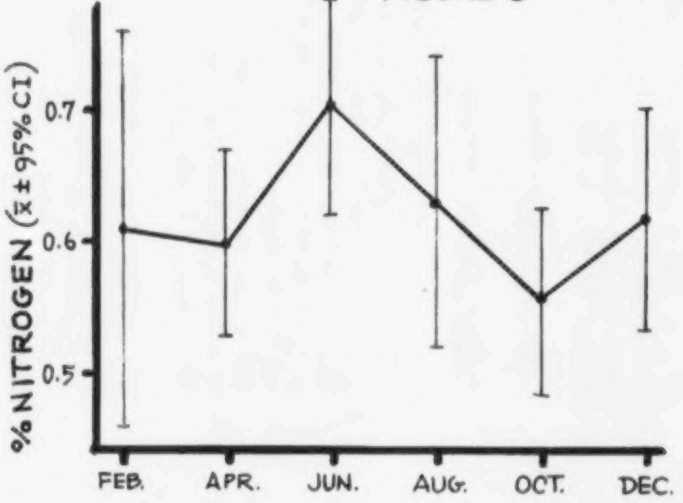


FIGURE 3



The increase in litter sample weight in August may be explained in one of two ways. This could be due to heterogeneity in the litter layer of the hardwood stand or there may have been an input of fresh litter in the system.

LITTER NUTRIENT DYNAMICS

Percent Carbon in Litter

In litter bag studies, the percent carbon in the litter is usually a constant (Wood, 1974; Bocock, 1963). This is not the case with unconfined litter (Figure 2). We believe that the increase in the percent carbon occur as a result of the selective removal of the more palatable litter, namely leaves, by invertebrates. This more palatable material would be characterized by a high nutrient content and a low percent carbon. Virtually all of the leaf litter had been removed by October of the sample year. The 47% carbon level reflects the branch litter.

The crease in the percent carbon in August coincides with the increase in sample weight previously noted. This indicates a litter input of low percent carbon material, such as flower parts, rather than sample heterogeneity. The relatively high percent carbon levels in October and December reflect the high rate of invertebrate activity of that particular fall; the fresh litter with a low carbon content and high nutrient content was selectively removed. Therefore the percent carbon values appear high in December.

Percent Nitrogen in Litter (Figure 3)

There are three sources of nitrogen input to the litter layer, other than litter fall. These are nitrogen fixation, insect frass, and rain fall (MacLean and Wein, 1978; Lousier and Parkinson, 1978). The nitrogen levels in the litter at any given time reflect the interaction of input and removal. Prior to June, the rate of input exceeds the rate of removal. With the increase of invertebrate activity in the summer, the rate of removal exceeds the rate of input. There is a large confidence interval around the average percent nitrogen level for February. This is evidence that the subnivian community is a mosaic of biologically active and inactive sites (Tardiff and Dindal, 1980). Sites with high microbial and invertebrate activity have higher nitrogen levels than areas with little or no activity.

These results are inconsistent with litter bag studies. With confined litter, the percent nitrogen continuously increases from various inputs (Anderson, 1973; Cragg et al., 1977; Gosz et al., 1973). The decline in the percent nitrogen in unconfined litter is due to the selective removal of nitrogen rich material by invertebrates. This activity is restricted by litter bags.

Litter C/N Ratio

The relationships of percent carbon to percent nitrogen (Figure

4) is relatively constant during the first four sample periods. This is evident also when comparing individual curves of percent carbon (Figure 2) and percent in nitrogen (Figure 3) with the C/N ratio curve. The drop in April is probably due to an increase in nitrogen from fixation coupled with a slow rate of removal by the low density spring invertebrate populations.

Litter bag studies using leaf litter only, usually show a decrease in C/N ratio as nitrogen is accumulated (Anderson, 1973; Cragg et al., 1977; Gosz et al., 1973: Wood, 1974). Likewise, in our study as the various components of leaf litter become enriched with nitrogen, and the C/N ratios of the leaves decrease, the invertebrate populations remove these components. However, since the net result is a proponderance of woody branch litter, the C/N ratio may appear to be constant or to increase temporarily. An example is the October C/N ratio which reflects the higher C/N ratio due mainly to branch litter.

Percent Calcium in Litter

Calcium in the litter may be thought of as originating from two different sources. First, calcium is a structural component of plant cells (Burges, 1956). Second, according to Chandler (1939), calcium is not retracted from leaves prior to litter fall. Therefore, there is a pooling of calcium in the leaves through the growing season which is reflected in the litter. These two phenomena explain the trend seen in Figure 5.

The initial high levels of calcium in February reflect the unretracted calcium pooled in the leaves prior to leaf crop. The large confidence interval about this point probably reflects the extent to which different tree species accumulate calcium in there leaves. The decline in percent calcium concentration covaries significantly with sample weight loss of the unconfined litter. This is consistent with litter bag studies (Burges, 1956; MacLean and Wein, 1978) and indicates that calcium is immobilized as a structural component in the litter until it is physically broken down.

LITTER NUTRIENT CORRELATION ANALYSIS (Table 1)

The variables available for litter correlation analysis are carbon, nitrogen, calcium, and litter sample weight. Both simple and partial correlations were calculated. The partial correlation reflects the relationship between the two variables of interest with the effects of othe other two variables removed. Simpson et al. (1960), Poole

CHARACTERISTICS of MIXED HARDWOOD FOREST LITTER

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FIGURE 4

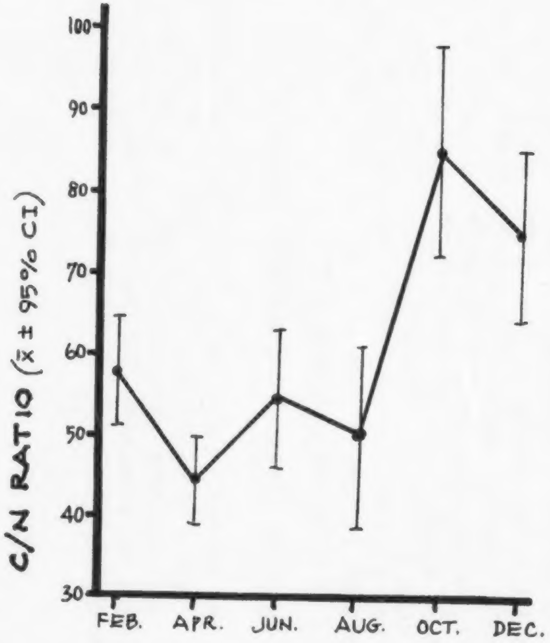

FIGURE 5

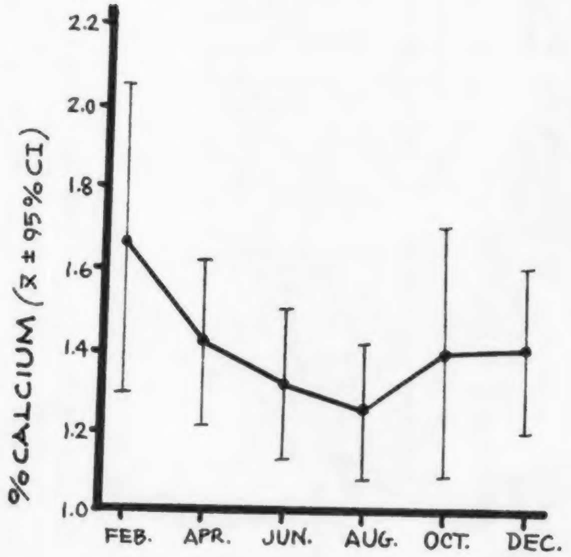

TABLE 1. LITTER NUTRIENT CORRELATIONS

Correlation	Simple Correlation	Partial Correlation
Sample WT:C	-.654	-.712
C:Ca	.178	.275
Sample WT:Ca	.142	.296
C:N	.294	.315

Correlations are significant at .250 (α=.05)

(1974), Snedecor and Cochran (1967) completely discuss this technique which has the advantage of showing the relationship between two variables after the effects of other dependent variables have been removed.

Litter Sample Weight related to Percent Carbon

Both the simple and partial correlations relating litter weight to percent carbon are negative and significant (Table 1). This correlation reflects the different decomposition rates of the constituents of the litter. The litter with a lower percent carbon concentration (mainly leaves) is decomposed and comminuted at a faster rate than the litter with a higher percent carbon concentration (branch litter). Consequently, as the sample weight decreases, the percent carbon in the remaining litter increases.

Percent Carbon related to Percent Calcium

The simple correlation of percents carbon to calcium is not significant; however, the partial correlation shows a significant relationship between these two variables when the effects of percent nitrogen and sample weight are removed (Table 1). Such a correlation is expected since it indicates that carbon and calcium are related as structural components in plant material.

Litter Sample Weight related to Percent Calcium

With these variables the partial correlation procedure indicates the relationship between sample weight loss and the loss of the calcium component which is accumulated in the leaves during growth. The covariation of calcium with carbon is not reflected in this partial correlation because the variation due to the carbon concentration has been statistically removed.

Percent Carbon related to Percent Nitrogen

The correlations represent a constant relationship between these two variables (Table 1). Correlations are mostly supported by the first four sample periods (Figure 4). Also, as noted before, this is not the case with litter bag data.

SOIL NUTRIENT TRENDS

It is immediately apparent from Figures 6-8 that carbon, nitrogen, and calcium are much less variable in the surface soil of the site than in the litter layer. Less variation is expected because: 1) these data were collected on only the top 10 cm of soil, and it is expected that much of the input from the litter as migrated via leaching and faunal activity to the lower soil horizons; and 2) the relative stability of these nutrient levels probably reflects a dynamic equilibrium between cation exchange capacity and plant root uptake.

The large confidence interval around the February nitrogen mean is probably due to the same mosaic effect noted for litter nitrogen. In sections of the surface soil where the microflora remain active throughout the winter, nitrogen is pooled. In areas where microflora were inactive, nitrogen was lost or was not mineralized.

SOIL NUTRIENT CORRECTION ANALYSIS (Table 2)

Percent Carbon related to Percent Calcium

As stated in the methods section, the calcium under consideration here is only the exchangeable component. These significant positive correlations reflect the probable interaction of calcium as a cation and the C.E.C. of humic material.

TABLE 2. SOIL NUTRIENT CORRELATIONS

Correlation	Simple Correlation	Partial Correlation
C:Ca	.530	.390
N:Ca	.872	.786
Ca:pH	.632	.441

Correlations are significant at .250 (α = .05)

Percent Nitrogen related to Percent Calcium

Lutz and Chandler (1946) reported that calcium in soils stimulates microfloral and faunal activity. This interaction is represented by the relatively high, positive correlations between percent nitrogen and percent calcium. As microfloral and faunal populations increase due to an increase in calcium, more nitrogen is immobilized.

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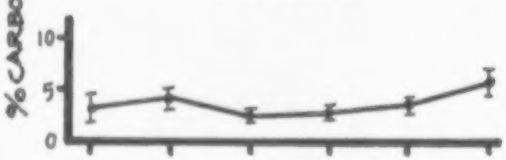
FIGURE 6

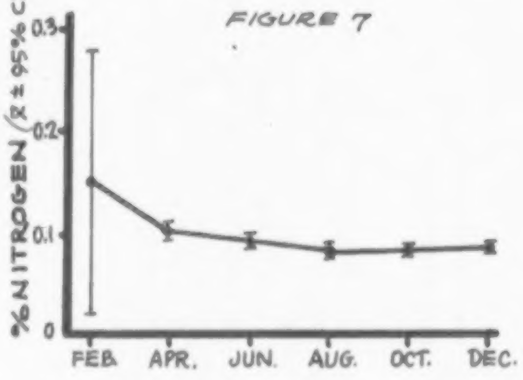
FIGURE 7

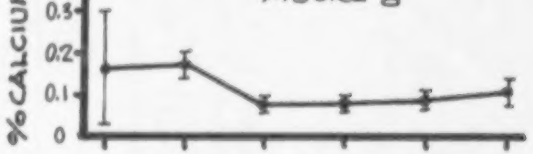
FIGURE 8

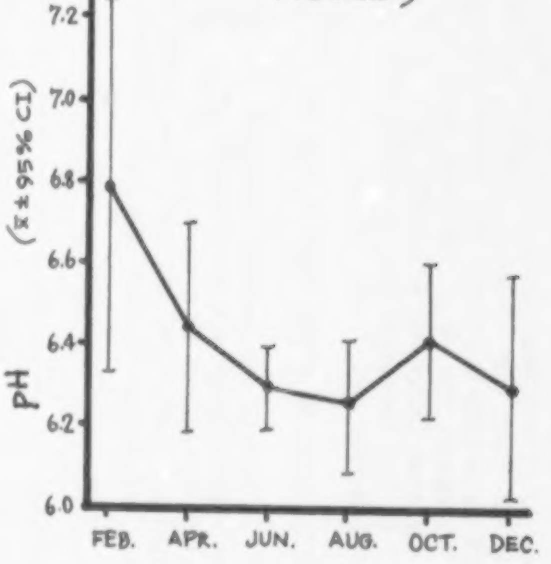
FIGURE 9

Percent Calcium related to pH

Three processes may potentially interact to produce these positive relationships (Table 2, Figures 8-9). First, calcium raises soil pH (Lutz and Chandler, 1946). Second, under anaerobic conditions, such as moisture saturation, microflora produce acidic metabolites which reduce the pH of the soil and result in leaching of cations such as calcium (Gray and Williams, 1971). Third, a soil pH change from 6.0 to 7.0 increases the solubility of calcium carbonate from 30% to 60% (Emerson and Green, 1938).

LITTER-SOIL NUTRIENT FLUX (Table 3)

Simple and partial correlations for litter:soil carbon, nitrogen, and calcium are not significant. The reason is that the litter and soil samples were collected at the same time, and these litter nutrient levels are not reflected instantaniously in the soil. The data were rearranged so that the soil nutrient information was compared with the nutrient information for the litter sampled the preceding period. This rearrangement showed nutrient levels in February litter to be correlated with those of April soil, nutrient levels in April litter to be correlated with those of June soil, and so forth. This shift produced better correlations representing the carbon and calcium fluxes. The nitrogen relationship did not improve because nitrogen moves through the system at a much faster rate than two months. The actual lag time for these nutrients could be determined with samples collected over shorter intervals.

TABLE 3. LITTER TO SOIL CORRELATIONS

Correlation	Without Shift	With Shift
C:C	.254	.361
Ca:Ca	.095	.255
N:N	-.118	-.008

Correlations are significant at .250 ($\alpha = .05$)

CONCLUSIONS

NUTRIENT TRENDS

1. Data show that weight loss in unconfined litter, in a mixed hardwood forest system, is linear.

2. Percent carbon in the total hardwood forest litter increases through the year. This is because litter of lower carbon content (leaf material) is decomposed at a faster rate than that with a higher carbon content (woody branch material).

3. Calcium loss is positively correlated with weight loss in the litter since calcium is a structural component of plant tissue.

4. Surface soil nutrient fluxes are of a much lower magnitude than litter nutrient fluxes.

CORRELATION ANALYSIS

1. Litter sample weight is inversely correlated with percent of carbon.

2. The percent carbon related to percent calcium correlation indicates that calcium is a structural component of litter.

3. Litter sample weight related to percent calcium reflects the loss of unretracted calcium accumulated prior to leaf drop.

4. Percent carbon related to percent nitrogen correlation indicates a relatively constant C:N ratio for most of the year.

5. The soil percent calcium related to pH correlation may be interpreted as a biological (Microbial metabolite and physical (solubility) relationship.

6. Percent soil nitrogen related to percent soil calcium reflects an increase in microbial activity with an increase in calcium, and therefore an increase in immobilized nitrogen.

ACKNOWLEDGMENTS

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KINETICS OF N-K INTERACTION AS RELATED TO STEM ROT INFECTION AND WATER HOLDING CAPACITY OF LEAF TISSUES OF TOMATO PLANTS

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Abstract:

Stem-rot infection followed by lodging and death of tomato plants occurred following abundant N fertilization. K fertilization was found to reduce the intensity of infection. The relationship between infection and N/K ratio in soil extract and whole plant tissues and moisture loss from excised leaves were outlined. K exerted a mixed type inhibition on the net influx of NH_4.

Introduction:

Abundant N fertilization was found to decrease the disease resistance of plants to soil born pathogens, as a result of rendering cell wall material more thinner as well as reducing the incrustation of cell walls with silicon and also increasing the concentration of the soluble amino acids and other palatable compounds (von Uexkull, 1976, Ismunadji, 1976 and Mitchell, et al. 1976). The form of N seems to have an effect on fungus infection, abundant NH_4-N nutrition was found to increase the infection (Barker, et al. 1967). Potassium, on the other hand, was found to increase the resistance of plants to fungus infection (Maynard, et al. 1968, Mengel, 1976, and Faizy, 1977).

The objectives of this study were to investigate the susceptability of tomato plants to stem rot infection by, naturally occurring, soil born pathogens as affected by different N and K fertilizers as well as its relationship to water loss from excised leaves and NH_4-K interaction.

Materials and Methods:

Tomato plants (Lycopersicum esculentum) were germinated in the field and transplanted (30 days old) to pots containing saline soil (pH = 8.5) from Kafr El Sheikh. The plants were fertilized with a split application each of 10.g of a mixture of ammonium nitrate, superphosphate and potassium sulfate fertilizers. The mixing was made up in the following ratios (of N P_2O_5 K_2O):

(a) 1 1 -, 2 1 -, 3 1 -, 5 1 -;

(b) - 1 2, 1.2 1 2, 2.4 1 2, 3.6 1 2, 4.8 1 2, 5.9 1 2;
(c) - 1 4, 1.2 1 4, 2.4 1 4, 3.6 1 4, 4.8 1 4, 5.9 1 4;
(d) 5 1 -, 5 1 2.1, 5 1 4, 5 1 6.4, 5 1 8.6, 5 1 10.7;

The first fertilizer application was made at 20 days after transplanting and the second one 30 days later. Five days after the first fertilizer application symptoms of stem rot infection (lodging followed by death) were apparent. The number of dead plants were calculated and % infection was obtained.

Two harvests were taken, the first was taken prior to addition of fertilizer and the second one 50 days later and at the same time soil samples were taken. Plant and soil analysis were carried out as outlined elsewhere (Faizy, 1978) and the net influx was estimated by the method of Brester and Tinker (1972).

The water loss was estimated by rapidly weighing leaves after excision and % loss in weight was calculated (g/g/min) after 10 minutes at noon.

Results and Discussions:

Unlike in other studies (Faizy, 1979)[5] made up on soil of the same area, NH_4 was the dominant form of N and no NO_3 was detected in the saturation soil extract.

The % of infected plants were hyperbolically increased with increasing the equivalent NH_4/K ratio in soil extract (fig. 1). Consequently the infection was similarly related to the equivalent N/K ratio in whole plant tissues (fig. 2). The resistance to stem rot infection was therefore increased by high K nutrition (Maynard, et al. 1968 and Mengel, 1976). One of the reasons for the induction of this resistance might be that K increased the synthesis of cell wall materials on the expense of soluble amino acids and thus cells would maintain a mechanical resistance against fungus invasion (Mengel, 1976) as well as low palatability.

An increase in water loss from excised leaves was observed with increasing the N/K ratio in plants (fig. 3). Similarly, transpiration rate was reduced in sugar beet with increasing K nutrition (Mengel and Forester, 1973). It was interesting to note that the % of infected plants were hyperbolically related to the water loss (fig. 4). The high water loss might be due to low protein content of cells (Stutt and Todd, 1969, Gusave, 1965) or high permeability of cell membranes (Mengel, 1976).

The influx of NH_4 was estimated in the absence of K (average endogeneous K concentration = 0.39 ± 0.10 me/100g at $t_{0.95}$) and in the presence of K fertilizers (average K concentration = 0.73± 0.09 me/100g at $t_{0.95}$ in saturation soil extract). The response curves were sigmoidal (Faizy, 1978 and 1979)[6] indicating the presence of at least two active sites per carrier enzyme. Using the Woolf-Augustinsson-Hofstee plot of the Hill equation

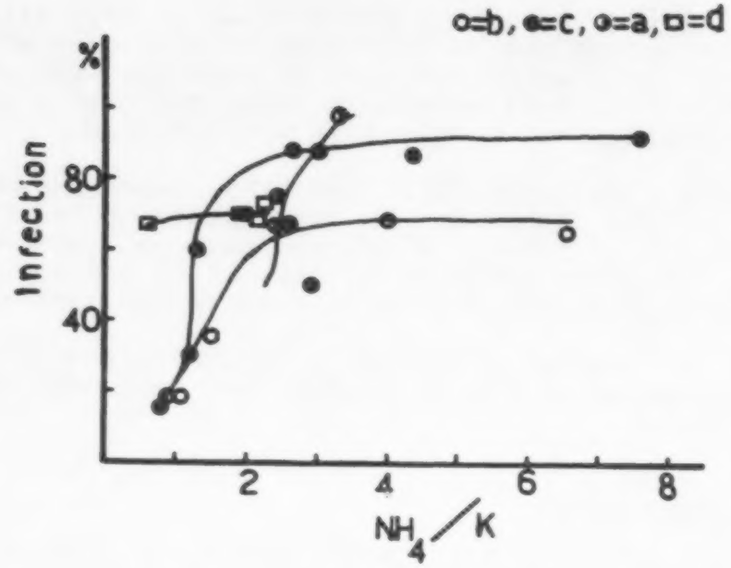

fig. 1 Stem-rot infection (%) as affected by the equivalent NH_4/K ratio in saturated soil extract with different treatments.

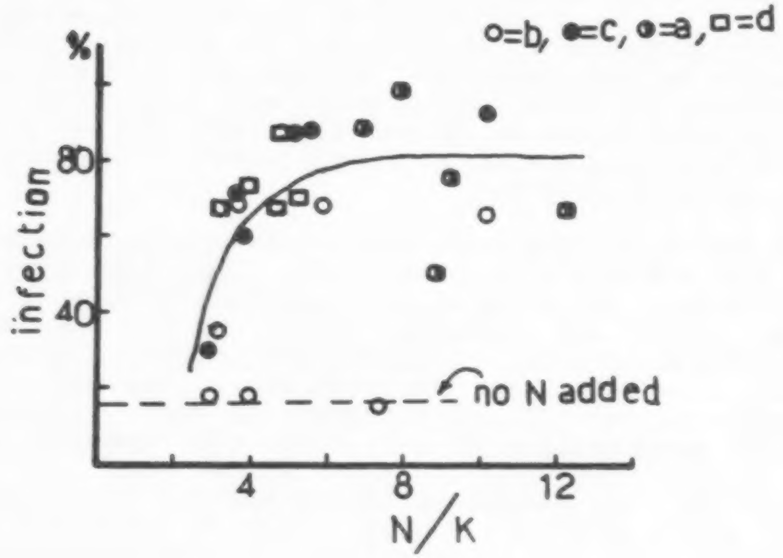

fig. 2 Stem-rot infection (%) as affected by the equivalent N/K ratio in whole plant tissues with different treatments.

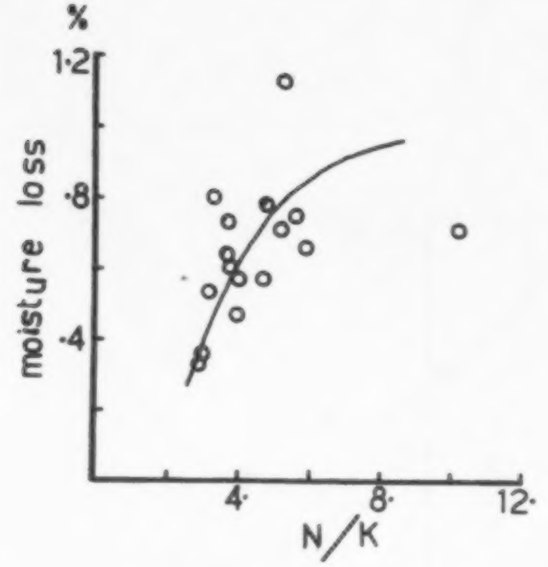

fig. 3 The percentage of moisture loss from excised leaves against the equivalent N/K ratio in whole plant tissues.

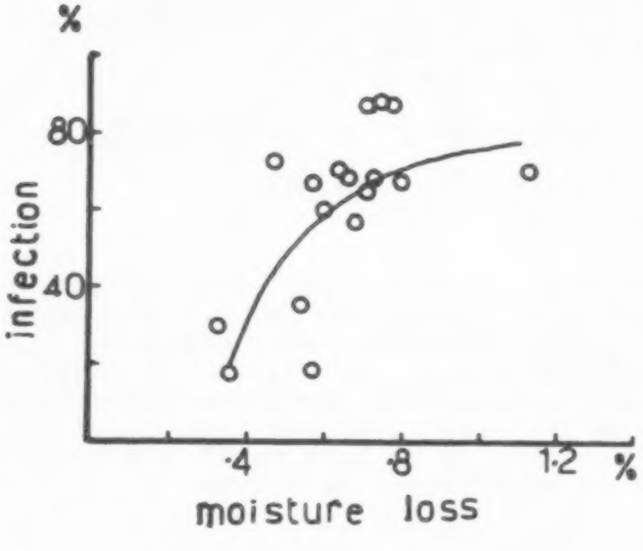

fig. 4 Stem-rot infection (%) as related to moisture loss from excised leaves.

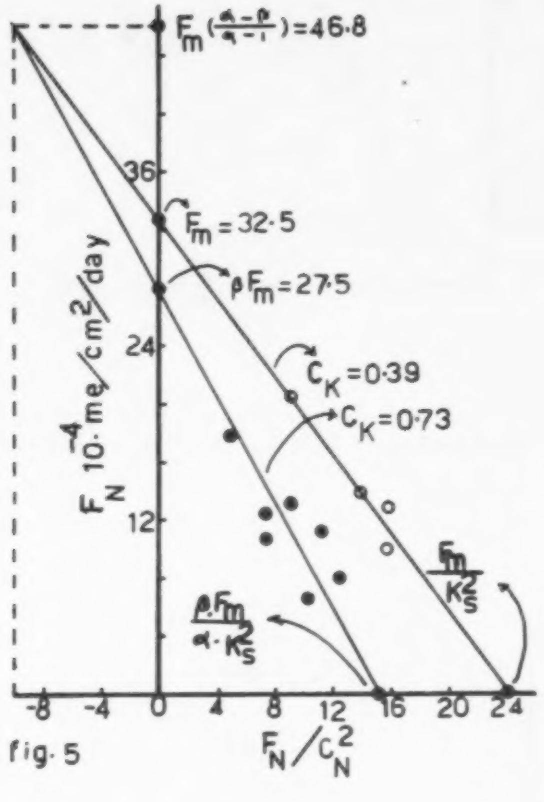

fig. 5

fig. 5 Woolf-Augustinsson-Hofstee plot, showing a mixed type inhibition of the NH_4 influx (F_N) by high concentration of K (C_k) in saturation soil extract. At low C_k the maximal theoretical NH_4 influx (F_m) was 32.5 and the affinity or substrate concentration at half maximal response (K_s) was 1.16. At high C_K, the F_m was inhibited by a factor of β = 0.85 to 27.5 and the K_s was inhibited by a factor α = 1.35

(Segel, 1975). Potassium was found to exert a mixed type inhibition on the maximal theoretical net NH_4 influx (3.25×10^{-6} E/cm^2/day) by a factor $\beta = 0.85$, and on the intrinsic dissociation constant by a factor of $\alpha = 1.35$ (fig. 5).

It was therefore concluded that plants can be made more disease resistance with K fertilizers; either directly through its physiological effects on cell constituents or indirectly by inhibiting the NH_4 influx. This conclusion might be of special importance to the Egyptian agriculture, especially after the construction of the Aswan Dam (1964) and the resultant decrease in K-replenishment of the soil.

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SULPHUR TRANSFORMATIONS IN OXYGEN-LIMITED SYSTEMS: SOILS, SEDIMENTS AND SLUDGES

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Sulfur is a major element essential to all life on earth. It is constantly being converted, transformed and transported between major organic and inorganic pools in both natural and anthropogenic systems. Both biochemical and geochemical pathways are involved in the cycling of sulfur between these pools in the biosphere, atmosphere, hydrosphere and pedosphere. In addition to its importance as a major biogeochemical element, atmospheric input of oxidized inorganic sulfur compounds derived from the combustion of fossil fuels has resulted in a major international research effort aimed at elucidating mechanisms and pathways of sulfur cycling.

Microorganisms play a major role in determining both the magnitude and rates of sulfur fluxes. Due to the diversity of metabolic pathways operating in natural microbial communities of sediments and soils, in situ microbiota are able to transform sulfur through all five of its oxidation states and to form a variety of inorganic and organic sulfur species. Biogenic evolution of sulfur compounds is the least well-known component of the global sulfur cycle; however, it appears that the majority of biogenic sulfur is evolved in the forms of hydrogen sulfide (H_2S) or dimethyl sulfide ($(CH_3)_2S$) (Hill, 1973; Moss, 1978).

Environmental conditions required for biogenic sulfide production are met in oxygen-limited, organic-rich systems such as intertidal marine sands, bogs, marshes, swamps, and their man-made analogs such as sewage sludge. Oxygen-limited systems are characterized by 1) a high moisture content, 2) a rapid microbial turnover of labile organic matter, 3) an adequate supply of organic or inorganic terminal electron acceptors, which may replace oxygen in microbial respiration, and 4) a dynamic redox gradient. The fourth characteristic is a consequence of the first three and is delineated by a zone of oxygen depletion.

The lower limit of this zone constitutes the redox discontinuity layer, where oxidizing processes become displaced by reducing processes (Fenchel and Riedl, 1970). By virtue of the dynamic interplay between net oxidation and reduction of nutrients by the natural microbial community, this zone represents the area of maximal bacterial activity and organic matter transformations (Kepkay et al., 1979). Below this zone, reduced products of anaerobic community metabolism accumulate; these products are toxic to most plants and animals and to many microorganisms. Oxygen depletion is due to the combination of low oxygen solubility in water, slow passive diffusion of oxygen into water-filled pores and rapid biological and chemical oxygen consumption. Systems which are intermittantly flooded, such as rice paddies and salt marches, are characterized by a vertical movement of the redox gradient. During periods of exposure and drainage, aerobic metabolism similar to that in aerobic soils proceeds, while during periods of submergence, anaerobic metabolism prevails (Ponnamperuma, 1972).

Bacterial Community Metabolism in Oxygen-Limited Systems.

Since the majority of metabolism in oxygen-limited systems is heterotrophic and anaerobic, bacteria are the primary agents in decomposition, although faunal constituents may serve an important role in altering bacterial activity (Abrams and Mitchell, this volume). The natural bacterial community in such systems can be divided into three functional groups, based on their respiratory metabolism: 1) facultative anaerobes, 2) obligate anaerobes and 3) fermentors. Respiratory reduction of a terminal electron acceptor such as oxygen or sulfate is directly coupled to the oxidation of a reduced carbon compound such as glucose; this coupling of oxidation-reduction reactions is required for biological transformation of energy into adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and yields carbon dioxide and reduced electron acceptors (e.g., H_2O, H_2S). Aerobic respiration, in which molecular oxygen (O_2) is reduced to H_2O, yields the maximum quantity of energy (in the form of ATP), per mole or organic reducing agent. Thus the facultatively anaerobic bacteria, which are widely distributed in O_2-limited systems, utilize O_2 as a terminal electron acceptor as long as a sufficient quantity is present. The lower limit of O_2 concentration which is required for aerobic respiration has been determined to be 3×10^{-6}M in several types of soils (Greenwood, 1961). When O_2 is present in lower quantities, facultative anaerobes switch to anaerobic respiration, utilizing nitrate as a terminal electron acceptor (Gambrell and Patrick, 1978).

The switch to anaerobic respiration has a profound impact on the chemical and physical environment, resulting in reduction of the surrounding substrate. The relative oxidizing and reducing potential of natural systems is indexed by the redox potential or Eh, a measure of the electron-escaping tendency of a reversible redox system (Zobell, 1946). In aqueous systems, the oxidation states of hydrogen, carbon, nitrogen, oxygen, sulfur and several metals are affected by Eh. O_2 becomes undetectable at an Eh of +350 mV. Below +330 mV, nitrate reduction may be initiated but this process is generally not marked above an Eh of +220 mV (Patrick and Delaune, 1977).

When nitrate becomes depleted, the metallic cations, oxidized manganese (Mn(IV)) and ferric iron (Fe(III)), are generally reduced in that order as electron-rich fermentation products accumulate. Fermentation differs from respiration in that the total energy-yielding redox reaction is intracellular and the electron acceptor is organic. Thus a reduced carbon compound such as glucose is catabolized to fermentation end-products such as ethanol, succinate, propionate and lactate (Doelle, 1969). Mn (IV) is reduced to Mn (II) at an Eh of about +250 mV, while Fe (III) is reduced to ferrous iron (Fe (II)) at about +125 mV. These metallic cations play a major role in poising Eh in natural systems and in determining the solubility of sulfur compounds.

In the sequential reduction of natural systems, the next major biological electron acceptor is sulfate. Sulfate reduction is carried out by a specialized group of obligate anaerobic bacteria, *Desulfovibrio*, *Desulfomonas* and *Desulfomaculum*, which reduce sulfate to sulfide in the Eh range of +115 to -450 mV, although an Eh of -95 mV and a pH greater than 5.0 is required for initiation of the process (Cappenberg, 1974; Zinder and Brock, 1978). The sulfate reducers generally carry out incomplete carbon metabolism, yielding acetate as well as CO_2 from substrates such as the fermentation products lactate, succinate, malate and ethanol. Dissimilatory reduction of sulfate to sulfide is a major mechanism governing sulfur metabolism in O_2-limited systems.

When most of the sulfate in mud or sludge has been utilized, and the Eh has dropped to less than -250 mV, CO_2 itself may serve as an electron acceptor and be reduced to methane (CH_4). Therefore, methanogenic bacteria are restricted to extremely reduced environments, utilizing low molecular weight organic acids, especially acetate, plus CO_2 and molecular hydrogen (H_2) to form CH_4 (Cappenberg, 1974). Reduction of CO_2 releases the smallest amount of energy per mole of reducing equivalent due to the high enthalpy of CH_4.

Not all of these sequential redox reactions may occur in a single O_2-limited system. For instance, soils and sediments which are permanently flooded may not exhibit denitrification since nitrate may not be present. However, all these reactions may be expected to occur in alternately flooded and drained systems or in reduced soils or sediments which are in contact with O_2 at the surface. All microbial metabolism follows similar pathways up to the point of pyruvate; beyond this point, the divergence of heterotrophic metabolism results in a variety of metabolic products (Wolin, 1974). During sequential oxidation of organic compounds, sulfur components are also metabolized and evolved in a manner dependent on availability and on oxidation state, as discussed in the next section.

Distribution of Sulfur Compounds in Soils, Sediments and Sludges.

Total sulfur content and major pools in three different systems are presented in Table 1. The soil data is based on studies of 37 surface agricultural soils in Iowa. The majority of sulfur in these soils occurs in organic form, primarily as ester sulfates, which include choline sulfate, phenolic sulfates and sulfated polysaccharides. The carbon-bonded component (C-S) consists primarily of the amino acids methionine and cysteine (Tabatabai and Bremner, 1972). The percentage of ester - SO_4 increased with depth in soils while the C-S fraction decreased.

TABLE 1. Major Sulfur Pools in Soils, Lake Sediments and Sludge

	Agricultural[1] Soil	Lake Sediment[2]		Sewage Sludge[3]	
		Oxidized	Reduced	Oxidized	Reduced
Total Sulfur ($\% \ g^{-1}$ dry wt)	0.03	0.16	0.13	1.10	1.22
Sulfur Pools: (% of Total Sulfur)					
SO_4^{2-}	1-5	42	0	11	7
$S\text{-}SO_3 + SO_3$	ND	ND	ND	13	30
FeS, S^{2-}, HS^-	ND	25	59	0	14
FeS_2, S^o	ND	0	21	ND	ND
Total Inorganic S	1-5	67	80	24	51
Ester-SO_4	31-63	ND	ND	37	5
C-S	3-20	ND	ND	39	45
Total Organic S	95-99	33	20	76	49

[1] Tabatabai and Bremner, 1972.

[2] Recalculated fron Nriagu and Coker, 1976.

[3] Waugh and Mitchell, in prep.

ND = no data

Although sulfur speciation in submerged soils has not been studied to the same extent, we can predict that at a pH near neutrality organic sulfur and sulfate would be dissimilated to H_2S, thiols and volatile organic sulfur and that H_2S would react with metallic cations to form insoluble sulfides (Ponnamperuma, 1972; Connell and Patrick, 1968). This type of speciation has been found in reduced sediments of Lake Ontario, where the surface sediments are oxidized and sediments deeper than six cm are reduced (Nriagu and Coker, 1976). The redox discontinuity layer occurred at 4 to 6 cm and this zone contained the highest concentration of total sulfur, over 65% of which was black, amorphous iron sulfide (FeS). Above this zone (0 to 2 cm), 25% of the total sulfur was in the form of FeS and below this zone (8 to 10 cm), 59% was present as FeS. In addition to FeS, pyrite (FeS_2) and elemental S (S^o) were present in reduced sediments. Unlike soils, less than half of the total sulfur can be accounted for as organic sulfur in lake sediments, due to the stability of inorganic oxidized and reduced sulfur.

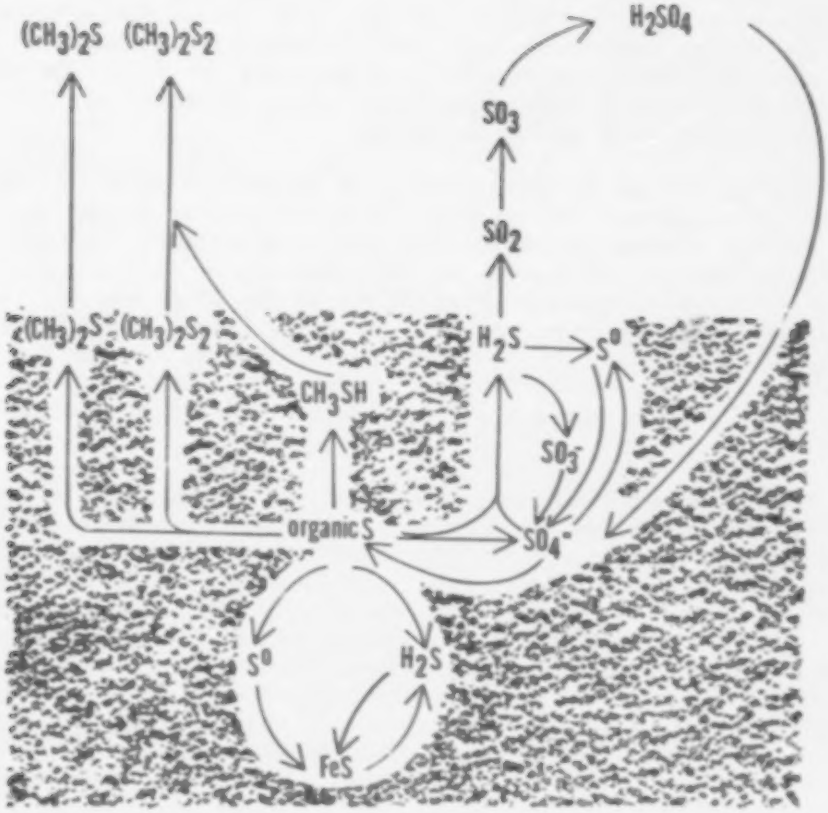
Sulfur speciation in aerobically digested sewage sludge has been studied in our laboratory and results concur with those of Sommers et al. (1977). The total sulfur content of sludge is one to two orders of magnitude greater than that in soils and sediments and speciation reflects the high initial quantity of organic sulfur. As would be predicted, oxidized sludge retains a large fraction of organic component, which is evenly divided between two major organic pools while the reduced sludge contains a low percentage of ester-SO_4 but a high percentage of thiosulfate ($S-SO_3$) and sulfite (SO_3). Although these two latter compounds are not found as intermediates in sulfate reduction, they may be stable intermediates resulting from polythionate reduction (Chambers and Trudinger, 1975; Doelle, 1969). The fraction of FeS in reduced sludge may initially appear to be too low when compared to reduced sediments, but the absolute concentration is far in excess of that occurring in sediments and is limited by the availability of ferric iron relative to sulfide. The excess of sulfide ions is demonstrated in the evolution of H_2S in sludge, as discussed in the next section.

Sulfur Transformations in Oxygen-Limited Systems.

Microbial sulfur transformations can be either assimilatory or dissimilatory. Bacteria are able to assimilate sulfur from a wide variety of inorganic and organic compounds for synthesis of the essential S-containing amino acids methionine and cysteine (Alexander, 1977). Under O_2-limited conditions, the primary S source is reduced organic S, derived from protein hydrolyses. In soils with low S content, such as agriculatural soils, sulfate immobilization in an organic form is the primary transformation. Since the major form of S in oxidized soils, ester-SO_4, is not available to plants, fertilizers are routinely used (Tabatabai and Bremner, 1972).

O_2-limited systems rich in organic material generally are not S-limited, since most of the organic material is derived from S-rich plant biomass. Freshwater macrophytes contain 0.8 to 1.0% S on a dry weight basis while phytoplankton contain 0.65% (Nriagu, 1968); bacteria generally contain 0.1 to 1.0% S (Alexander, 1977). The majority of S transformations in O_2-limited systems result in production of volatile inorganic or organic sulfides; see Figure 1. Sulfides may be released as H_2S, or bound as metallic sulfides, depending on the availability of cations (Ponnamperuma, 1972). Pyrite formation occurs in reduced sediments when ferric sulfides are undersaturated and soluble sulfides are present (Howarth, 1979).

FIGURE 1. Major microbial sulfur transformations in oxygen-limited systems.



$(CH_3)_2S$
$(CH_3)_2S_2$
H_2SO_4
SO_3
SO_2
$(CH_3)_2S$
$(CH_3)_2S_2$
H_2S
S^0
CH_3SH
SO_3^-
organic S
$SO_4^=$
S^0
H_2S
FeS

In saltmarsh sediments, where sulfate levels are very high (approximately 28 mM), sulfate reduction is not controlled by sulfate supply but by temperature, H_2 availability and nutrients, especially lactate (Nedwell and Abram, 1979; Rees, 1973). In freshwater marshes and submerged soils, where the sulfate concentration is below the level necessary to saturate enzyme activation sites, sulfate reduction is limited primarily by sulfate concentration. Diffusion rates of H_2S from flooded soils, sediments and sludges depend not only supersaturation of metallic cations, but also on diffusion and mass flow (Kleiber and Blackburn, 1978). Respiration rates of very reduced systems, such as sewage sludge, are controlled in part by outward diffusion of reduced products which are toxic if concentrated (McDonnell and Hall, 1969).

Evolved H_2S may be biologically or chemically oxidized. These oxidized compounds may combine with atmospheric water and be returned to the earth's surface in the form of acid precipitation (Likens and Bormann, 1974). Alternatively, sulfides may be biologically oxidized to sulfates and elemental sulfur by the chemoautotrophic bacteria Thiobacillus or by the photosynthetic bacteria Chlorobium and Chromatium (Doelle, 1969). Elemental sulfur may then be further oxidized to sulfite, thiosulfate and sulfate by other members of Thiobacillus or serve as an electron acceptor, as can sulfite and thiosulfate.

H_2S can also be released in dissimilatory metabolism of organic sulfur compounds, as can the volatile organic sulfides methane thiol (CH_3SH), dimethyl sulfide (($(CH_3)_2S$, dimethyl disulfide ($(CH_3)_2S_2$), carbon disulfide (CS_2) and carbonyl sulfide (COS), as noted in Table 2. $(CH_3)_2S_2$ is formed as an oxidation product of CH_3SH (Segal and Starkey, 1969). Organic sulfide evolution in oxidized soils occurs generally when the organic content is greater than 5% on a dry weight basis (Banwart and Bremner, 1976a). However, when oxidized soils are waterlogged, even those with low organic content evolve sulfides, primarily in the forms of CH_3SH and $(CH_3)_2S$. Thus organic sulfide evolution is not restricted to reduced systems but is enhanced by O_2-limitation.

TABLE 2. Volatile Sulfur Compounds Released from Soils, Sludge-Amended Soil and Sludge

Sample Type	Organic Matter (%)	Treatment	
Belinda[1] Silt Loam	2.17	A	None
		W	CH_3SCH_3
Sharpsburg[1] Silty Clay Loam	3.91	A	None
		W	CH_3SCH_3, CH_3SSCH_3

TABLE 2. (Continued) Volatile Sulfur Compounds Released From Soils, Sludge-Amended Soil and Sludge

Sample Type	Organic Matter (%)	Treatment	
Hayden[1] Sandy Loam	5.78	A	CH_3SCH_3
		W	CH_3SCH_3
Okoboji[1] Silty Clay Loam	12.1	A	None
		W	CH_3SCH_3
Soil + Sludge[2]		A	CH_3SCH_3, CH_3SSCH_3
		W	CH_3SH, CH_3SCH_3, CH_3SSCH_3
Sandy Soil + Sludge[2]		A	CH_3SSCH_3, CS_2
		W	CH_3SH, CH_3SCH_3, CH_3SSCH_3, COS, CS_2
Sludge[3]	60	A	H_2S, CH_3SH, CH_3SCH_3
		W	H_2S, CH_3SH, CH_3SCH_3, CH_3SSCH_3

[1] Banwart and Bremner, 1976a.

[2] Banwart and Bremner, 1976b.

[3] Hornor, in prep.

A = Aerobic

W = Water-logged

Sludge-amended soils evolve a variety of organic sulfides under both aerobic and water-logged conditions. Sludge alone evolves these compounds as well as H_2S under similar incubation conditions. The little that is known about the mechanisms and organisms responsible for evolution of these compounds in soils and sludges is derived from pure culture work and from sulfur-amended soils and sludges (Bremner and Steele, 1978). The primary organic sulfur source for H_2S formation is cysteine, while the majority of the organic sulfides are derived from methionine (Francis et al., 1975). Several bacterial isolates including *Clostridium*, *Pseudomonas* and *Achromobacter* have been found to dissimilate methionine to volatile sulfides (Segal and Starkey, 1969; Alexander, 1974). Additionally actinomycetes, yeasts and higher fungi have been shown to evolve these compounds (Kadota and Ishida, 1972).

CH_3SH has received more attention than other volatile sulfides due to its powerful and offensive odor and phytotoxic properties; this gas, as well as H_2S, may accumulate in soils of rice paddies and cause rice root damage (Alexander, 1974; Joshi and Hollis, 1977). The sulfur-oxidizing bacterium Beggiatoa, occurring naturally in rice paddies, is able to detoxify these sulfides. H_2S is also toxic to nematodes (Rodriguez-Kabana et al., 1965) and developing fish eggs and fry (Smith and Oseid, 1972).

Burrowing by invertebrates exerts a profound influence on nutrient cycling and decomposition in heterotrophic systems. Invertebrates may stimulate microbial activity and decomposition by a number of mechanisms including comminution, removal of senescent colonies, enrichment by nitrogenous excretions, elimination of antibiotic metabolites, enhancement of oxygen penetration, and addition of mineral nutrients. These effects occur in soils (Syers et al., 1979; Kitchell et al., 1979), sediments (Fenchel and Harrison, 1976) and sludges (Mitchell et al., 1977; Abrams and Mitchell, this volume). In O_2-limited systems, burrowing activities, or bioturbation of sediments and soils, may markedly increase substrate oxidation, altering redox gradients that control many mineralization processes and redistribute nutrients across system strata (Kitchell et al., 1979; Withers, 1978).

The major mechanisms by which fauna may influence sulfur biogeochemistry are through either a direct effect on the microflora or through physical and chemical alteration of the surrounding environment. Although there is little data on the specific roles which animals play in modifying sulfur compounds, there is evidence that a sediment-dwelling polychaete worm stimulated rates of microbial sulfate reduction and increased solubility of metallic cations (Aller and Yingst, 1978). In contrast, Hornor and Mitchell (in review) have shown that earthworm feeding may decrease rates of sulfide evolution in sludge. Also, interstitial metazoans are able to actively scavenge sulfide ions in sediment pore water, detoxify the sulfide and release it back into the surrounding environment (Powell et al., 1979).

The most striking difference between aerobic and anaerobic decomposition is the nature of the metabolic products released. In a normal, well-drained soil, the primary products of microbial decomposition are carbon dioxide, nitrate, sulfate and refractory humus-like material. In submerged or waterlogged soils, sediments and sludge, carbon dioxide, methane, ammonia, hydrogen sulfide, and volatile organic sulfides such as methane thiol, dimethyl sulfide and dimethyl disulfide plus refractory peat-like organic material predominate. Due to absorption of H_2S in systems with low total sulfur content and high metallic cation concentrations, such as soils and oxidized sediments, H_2S is produced but not evolved.

In aerated soils, sediments and sludges, the major microbial S transformations are 1) oxidation of elemental sulfur, sulfide and organic sulfur to sulfate and 2) assimilatory reduction of sulfate into biomass. In O_2-limited systems, the major transformations are 1) dissimilatory sulfate reduction to sulfide and 2) dissimilation of S-containing amino acids methionine and cysteine (derived from protein hydrolysis) to H_2S, thiols and volatile organic sulfides. A diverse, ubiquitous microflora capable of transforming S through all of its oxidation states is present in O_2-limited systems. Microbial community S transformations are controlled by several environmental parameters, including Eh, pH, the availability of labile organic compounds serving as electron donors and the availability of inorganic electron acceptors.

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ON THE INCIDENCE AND DISTRIBUTION OF PARASITES OF SOIL FAUNA OF MIXED CONIFEROUS FORESTS, MIXED LEAF FORESTS, AND PURE BEECH FORESTS OF LOWER SAXONY, WEST GERMANY

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INTRODUCTION

It is well known that the soil fauna are important in the formation of the earth's soils. Soil fauna, their population densities and characteristics have been studied by different authors in the recent years. But practically no data exist concerning their pathology and parasitic diseases. This study is the first major contribution on incidence and distribution of parasites belonging to different groups of the microorganisms found in natural populations of soil fauna from a spruce forest of Lower Saxony, West Germany.

MATERIAL AND METHODS

The forest organic soil samples used in examinations of the soil fauna were collected during 1978 and 1979 in 21 different localities in mixed coniferous forests (pine, Scoth pine, and larch as primary trees), mixed deciduous forests (beech, elm and oak as primary trees), and pure beech forests, mainly in Lower Saxony, West Germany.

Samples containing 8478 specimens were extracted via modified Tullgren extractors. Larvae, pupae, and adults were first separated and then studied individually under light microscope. Adults were dissected and their organs as well as eggs were isolated before being studied intensively. They were smeared dry on slides, fixed with methanol or Bouin's fluid and stained with Giemsa-Romanovsky or Heidenhain's iron haematoxylin solutions. Usually the contents of the body of an infected animal were sufficient enought for the preparation of one smear. For staining nuclei of the spores of pathogens, a small spot of stained smear was treated with a droplet of the 1% HCL, and the droplet was heated for about a minute over a flame until a bubble appeared. The smear then was washed with cold water and stained again with Giemsa solution for 1-2 min. The developmental stages of parasites and their sizes were evaluated in smears of freshly dissected material as mellas fixed-stained preparations using an ocular micrometer.

Only the heavily infected parts of the host could be fixed in situ and the organs prepared in the usual way for embedding into epon-araldite for study with electron microscope. The tissues of infected animals were fixed at 4°C for 2 hrs. in 2% glutaraldehyde and postfixed in 2% osmium tetroxide, each being dissolved in 0.1 M cacodylate buffer (pH 7.4). Tissues of infected animals were then bulk stained for 14 hrs. in 3% aqueous uranyl acetate followed by routine dehydration (60 to 100% Ethanol), and embedded in epon-araldite. Thin sections (400-500Å) were cut with LKB ultramicrotome (Ultratome III) and stained in uranyl acetate and lead citrate. Micro-photographs were taken with a Philips 301 Electron Microscope.

RESULTS

Major parasitic and pathoganic components of the 8478 specimens of soil fauna judged by their abundance, frequency and biotopes are shown in Table 1. and 2. Three groups of decomposers: oligochaete, acarines, and collembolans were intensively studied as organisms in which the high numbers present in the samples and their intensity of transformation of organic materials in forest soils plays an important role in nature. The highest infection level for these groups occurred in mixed leaf forests (Table 1). The lowest percentage of infections was in mixed coniferous forests. The pure beech forests lie in between. These data show that there is a considerable difference between deciduous and coniferous forests. These differences may be due to the differences in the occurence of variety of fauna and higher density of their population within broad-leaf forests compared to coniferous forests

Table 1. THE SURVEY AND INCIDENCE OF PARASITES OF SOIL FAUNA OF LOWER SAXONY, W. GERMANY, 1978 - 1979.

Host Animals	TOTAL: No. Ex.	% Inf.	BIOTOPES: Pure beech forests	Mixed deciduous forests	Mixed coniferous forests
ANNELIDA					
Oligochaeta	480	54	16	32	6
ARANEIDA					
Acarina	2600	42	11	23	8
MYRIOAPODA	110	-	-	-	-
INSECTA					
Apterygota	2100	7	2	4	1
Orthoptera	52	6	1	5	-
Rhynchota	64	7	3	4	-
Coleoptera	560	22	6	14	2
Hymenoptera	52	12	3	5	4
Diptera	340	16	5	8	3
Lepidoptera	120	28	7	15	6

Results obtained from the studies of parasites occurring in all group of animals show that the population densities of soil fauna of spruce forest soils of Lower Saxony were found to be infected by nematodes, and four groups of microorganisms: viruses, bacteria, fungi, and protozoa (Table 2).

Table 2. THE PERCENT OCCURENCE OF DIFFERENT GROUP OF PARASITES FOUND IN THE SOIL FAUNA OF LOWER SAXONY, W. GERMANY 1978 - 1979.

	Total:	Types of Parasites:				Protozoa	
	% Inf.	Nematodes	Virus	Bacteria	Fungi	Rhizopoda	Sporozoa
ANNELIDA							
Oligochaeta	54	-	-	-	15	2	34
ARANEIDA							
Acarina	42	1	-	2	6	-	33
MYRIOAPODA	-	-	-	-	-	-	-
INSECTA							
Apterygota	7	-	-	-	4	-	3
Orthoptera	6	-	-	-	6	-	-
Rhynchota	7	-	-	-	7	-	-
Coleoptera	22	2	-	-	17	-	3
Hymenoptera	12	3	-	-	9	-	-
Diptera	16	-	-	-	10	2	4
Lepidoptera	28	2	3	1	22	-	-

The highest level of infection in three group of decomposers was caused by protozoans and fungi. Nematodes and bacteria were found rarely as parasites of decomposers. For other groups of insects the most infections were caused by Fungi, Protozoa, and the Nematodes

Many important genera were found to be pathogenic in Arthropoda and they were distributed within the 21 localities examined. (Table 3) In Acarina (Table 3), generally the genus Gregarina showed the highest level of infection in all localities. There was a little difference between the

Table 3. THE PERCENT DISTRIBUTION OF IMPORTANT GENERA OF FUNGI AND SPOROZOA (PROTOZOA) OF ORIBATEI (ACARINA) AND COLLEMBOLA INVESTIGATED IN DIFFERENT LOCALITIES OF LOWER SAXONY, W. GERMANY, 1978 - 1979.

	LOCALITIES																				
	MIXED CONIFEROUS FORESTS									PURE BEECH FORESTS						MIXED DECIDUOUS FORESTS					
PARASITE GENERA FOUND IN ORIBATEI (ACARINA)	Trelde	Sohlingen	Bovenden	Lonau	Adelebsen	Gartow	Lüneburg	Celle	Uelzen	Schieringen	Einbeck	Uslar	Salzgitter-Bad	Hameln	Rodetal	Dassel	Bergsdorf	Bergen	Rosengarten	Bleckede	Lutter
SPOROZOA																					
Helicosporidium	--	--	--	--	--	--	3	--	--	--	--	--	2	--	--	--	--	3	--	--	--
Gregarina	8	31	2	7	--	--	33	31	36	6	30	16	28	18	10	30	20	31	26	39	14
Nosema	--	1	--	6	--	--	5	4	2	--	3	5	2	2	7	3	--	2	2	2	5
Pleistophora	6	1	--	--	--	--	--	--	--	--	2	5	3	--	--	3	--	2	2	2	--
Thelohania	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	1	--	1	--	--	--
Haplosporida*	12	17	--	--	--	--	14	12	16	--	11	--	18	20	10	19	18	15	--	16	19
PARASITIC GENERA FOUND IN COLLEMBOLA																					
FUNGI																					
Entomophtora	--	--	--	--	--	--	--	--	3	--	2	--	--	--	--	--	2	2	3	--	--
SPOROZOA																					
Gregarina	--	--	--	--	--	--	--	--	--	--	--	--	3	--	--	--	-4	--	--	6	--
Adelina ?	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	--	--
Nosema	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	5	--	5	2	--	--
Thelohania	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	2	--	2	--	--
Auraspora gen. nov.	--	--	--	--	--	--	--	2	--	--	--	--	--	--	---	--	--	--	1	--	--
Encephalitozoon	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--

* organisms like Haplosporida

mixed leaf forests (18%), and mixed coniferous forests (16%). The highest level of infection by different species of Haplosporidia (?) was again confined to mixed leaf forests (14.5%) and the lowest in mixed coniferous forests (8%), For different genera of Microsporidia including Nosema spp., Thelohania spp., and Auraspora gen. nov. the highest level of infection was found in pure beech forests (1.8%), followed by the mixed deciduous forests (1.4%), and mixed coniferous forests (1%). The Helicosporidium parasiticum Keilin, was found only in three localities. In the localities of Fartow and Adelebsen the infections were totally absent. The percentage of infections by pathogenic genera in Collembola was generally low, with very few found in any of the localities investigated. In comparison, Sporozoa (Protozoa) infected several groups of decomposers including the Oligochaeta and species of moss-mites and Collembola (Table 4).

DISCUSSION

The results presented in this paper are of a preliminary nature and more work is called for, although efforts have been made to identify the parasites, particularly their family, genera, and in some cases the species of Fungi, and Sporozoa.

Our work raises certain important questions which need immediate attention as very little work has been published (Meier 1956, Stammer 1961) on the pathology and diseases of soil fauna. However, we have only established microsporidian infections in two species of moss-mites Rhysotritia ardua C. L. Koch (Fam. Euphtiracaridae) and Hermania gibbs C. L.Koch (Fam. Hermaniidae) (Purrini and Baumler 1977, 1978), but have also recorded a large number of new species of different groups of microorganisms (Purrini 1976, 1979; Purrini and Weiser 1979; Purrini, Bukva and Baumler 1979). The present study presents some data on all groups of decomposers found in natural populations of soil fauna in forest soils.

Nematodes, Viruses, Bacteria, Fungi, and Protozoa, were found in all of the materials investigated. Most of the infections was found in the cells of the fat bodies, body cavity, and also from muscles, ovaries, eggs, male gonads, and intestingal epithelium of hosts (Figures 1-45). In all, 14 different parasites were found in oligochaeta, of which 11 species belong to the Family Monocystidae (Eugregarinida, Sporozoa, Figures 1-6). One parasite was close to the genus Helicosporidium (**Helicosporida, Protozoa**) (Figures 7,8), and two belong to the genus Nosema (Microsporida , Sporozoa) (Figures 8,9,10). Of those, Helicosporidium parasiticum, 7 species of Family Monocystidae, and two of Nosema spp. are new for the Oligochaeta.

Some of the important pathogens of moss-mites are presented in Figures 11-19 and 44,45. There were 9 species of Microsporida , of which 6 belong to the genus Nosema (Figure 18), two are Pelistophora species (Figure 19), and a Thelohania species was found. Eight species belonging to Sporozoa (Protozoa) were from genus Gregarina (Eugregarinida, Sporozoa, Figure 17); one was a member of Class Ciliata (Protozoa, Figure 16), and the remaining two were H. parasiticum (Figures 12,13) and Nematodes (Figure 11).

Light microscopy:

Figs. 1-10: *OLIGOCHAETA* /Figs. 1,2,3,4,5,6, and 6a: fresh condidition;
7: Heidenhains iron haematoxylin stain;
8,9: Phaco;10: Giemsa stain/

1. *Apolocystis villosa*, adulte trophozoits in body cavity, 300 x.
2. Syzygy of *A. villosa* in body cavity, 750 x.
3. *Oligochaetocystis spp.*, the young cysts in body cavity, 300 x.
4. *Oligochatocystis spp.*, two trophozoits in pairs, body cavity, 1200 x.

5a. *Oligochaetocystis spp.*, free trophozoits in pairs; 5b. free trophozoit of *Apolocystis spp.*, 300 x.

6. *Monocystis spp.*, the mature sporocysts in fat body, 3000 x.

6a. *Nematocystis spp.*, the mature sporocysts in fat body, 3000 x.

7. *Helicosporidium parasiticum*, free mature spores, 3000 x.
8. *Nosema spp.*,and *H. parasiticum*, mixed infection; mature spores of both parasites in fat body, 1200 x.
9. *Nosema spp.*, mature spores in fat body, 1200 x.
10. *Nosema spp.*, mature spores in fat body, 3000 x.

200 myu (Fig. 2)

400 myu (Fig.1,3,5)

45 myu (Fig.8,9)

50 myu (Fig.6,6a,7,10)

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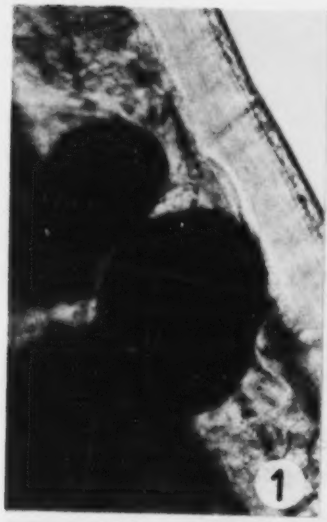
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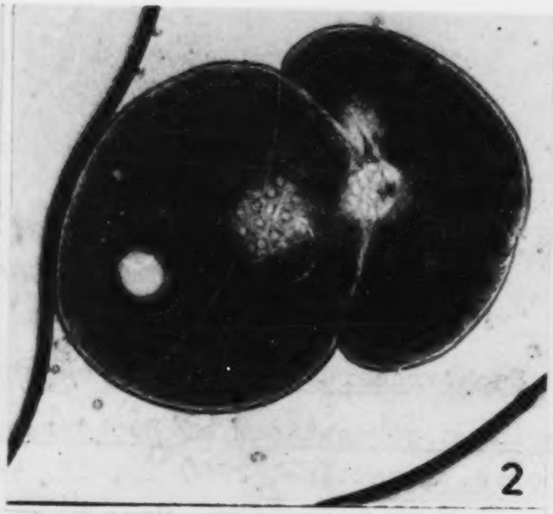
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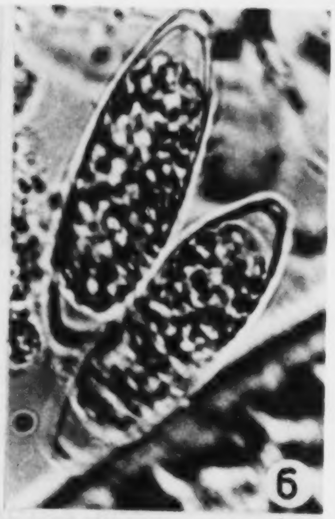
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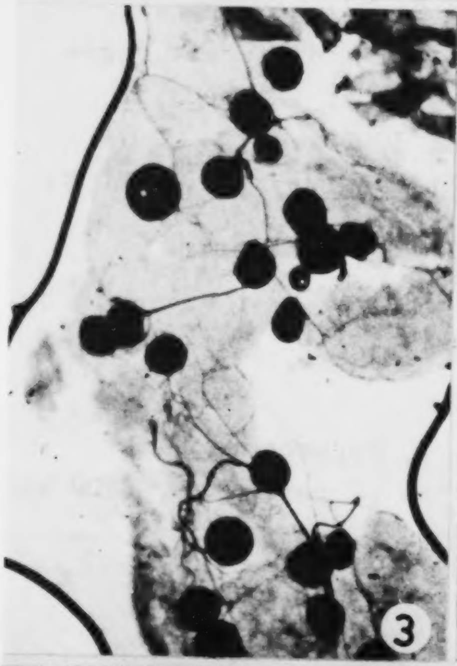
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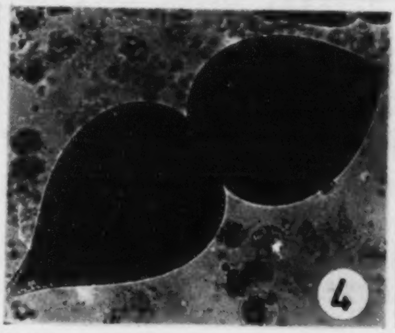
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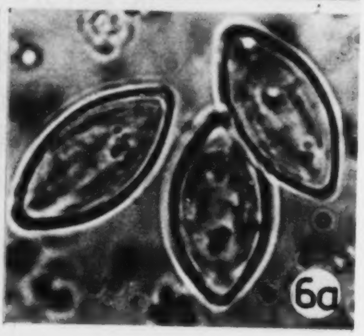
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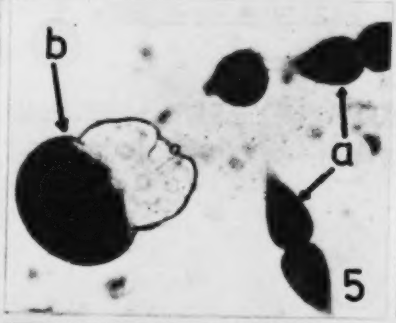

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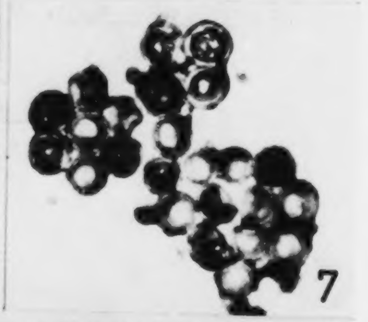
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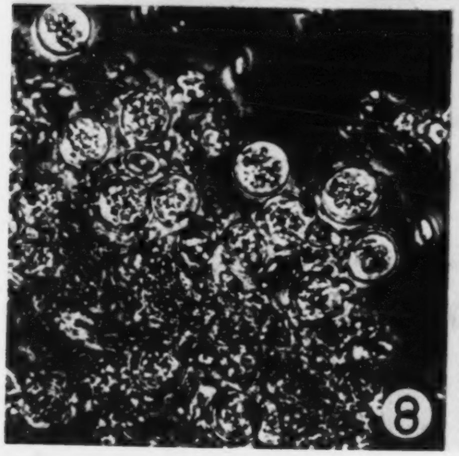
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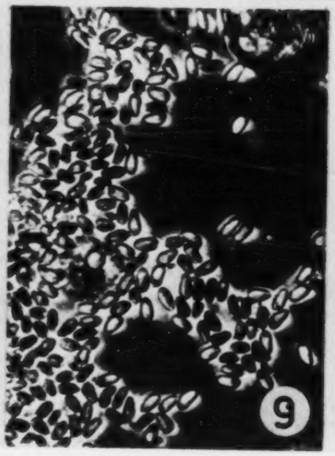
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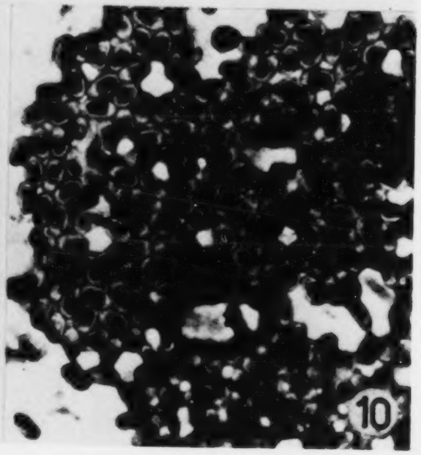
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Figs. 11-19: ORIBATEI /Figs. 1,17: fresh condition; 12,19: phaco; 13,14,15, and 16: Heidenhains iron haematoxylin stain; 18: Giemsa stain/

11. Nematodes of Euphtyracarus spp., body cavity, 300 x.

12,13. Helicosporidium parasiticum of Euphtyracarus spp., 12. mature spores, intestine, 1200 x.; 13. vegetative stages and mature spores, intestine, 3000 x.

14,15. Haplosporidia ? of Damaeus clavipes; 14. different vegetative stages in Nephrocyts, and cells of fat body in Caecum, 3000 x.; 15. Mature spores, 3000 x.

16. Ciliata, cilia in body cavity of Euphtyracarus spp., 3000 x.

17. Gregarina spp. of Steganacarus applicatus, two mature gamonts, intestine, 1200 x.

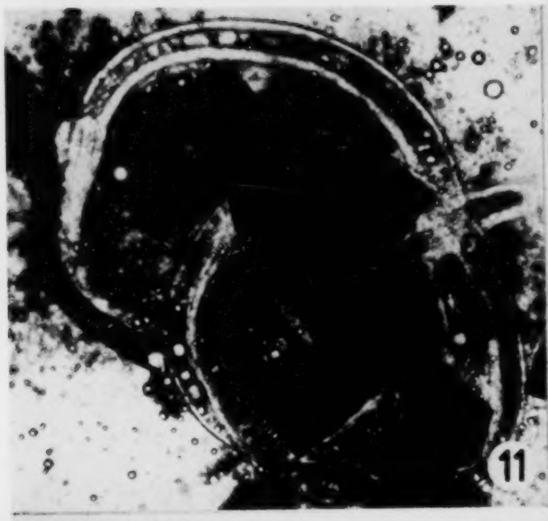
18. Nosema spp. of Damaeus onustus, mature spores in fat body, 3000 x.

19. Pleistophora spp. in Microtitia minima, nephrocyts full with vegetative stages and young spores of parasites, 1200 x.

450 mμ (Fig.11)

45 mμ (Fig. 13,14,15,16,18)

60 mμ (Fig. 12,17)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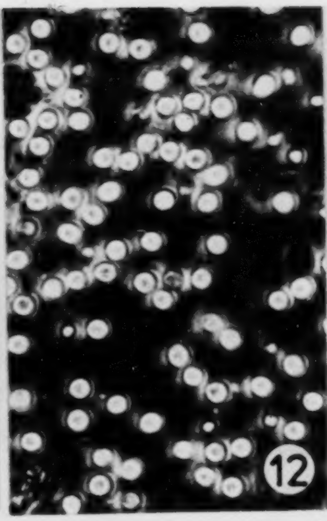
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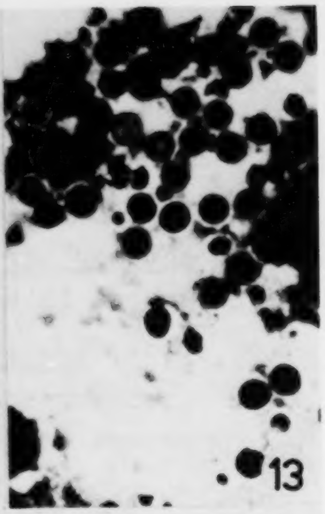
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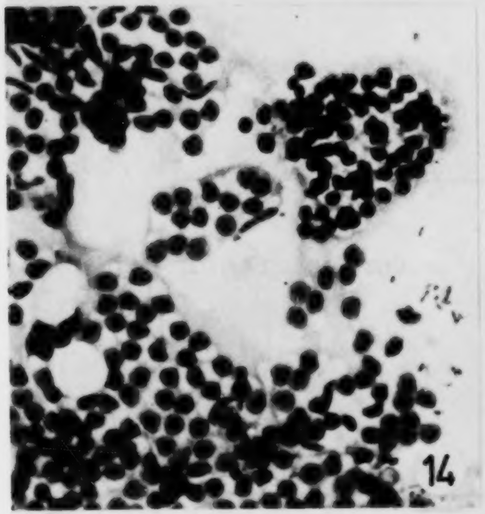
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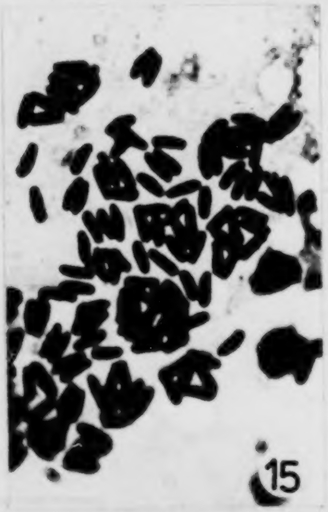
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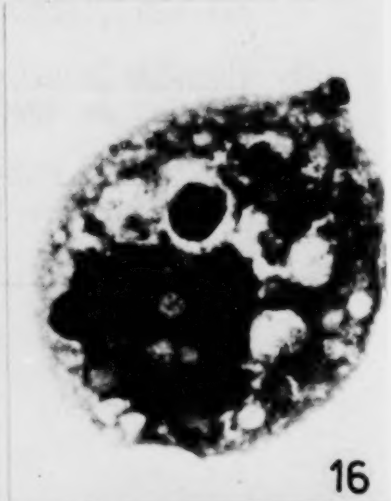
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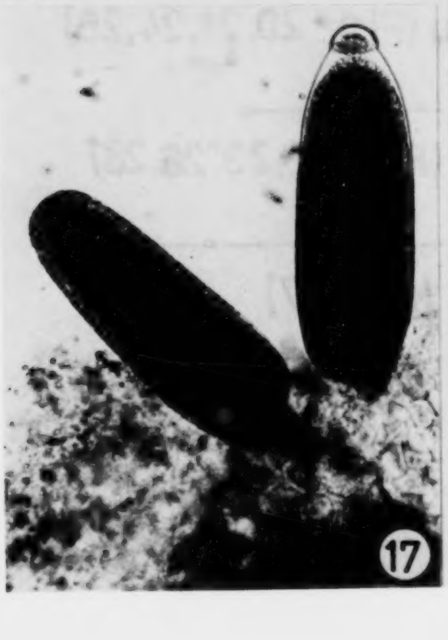
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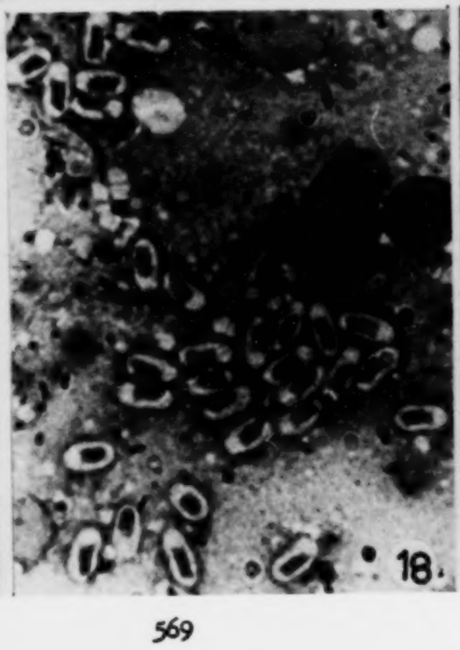
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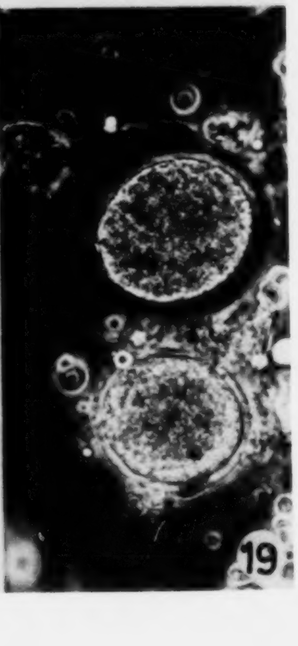
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Figs. 20-28: *COLLEMBOLA* /Figs. 20,22, and 23: fresh condition; 21,24, and 25: phaco; 26,27, and 28: Giemsa stain/

20. *Entomophtora spp*. of *Tomocerus flavescens*, conidia and spores in body cavity, 750 x.

21,22,23. *Adelina spp*.? of *Neanura muscorum*, in fat body; 21. premature cysts, 1200 x; 22. premature cyst, 3000 x; 23. mature cyst with sporocysts, 3000 x.

24,25. *Nosema spp*. of *Lepidocyrtus cyaneus*, mature spores in fat body, 1200 x.

26. *Thelohania spp*. of *T. flavescens*, different **vegetative** **stages** and mature spores in fat body, 3000 x.

27. *Thelohania spp*. of *Lepidocyrtus lignorum*, sporoblasts with mature spores in fat body, 4000 x.

28. *Auraspora gen. nov*. of *L. lignorum*, mature spores in gonads, 3000 x.

100 mμ (Fig. 20,21,24,25)

50 mμ (Fig. 22,23.26,28)

50 mμ (Fig. 27)

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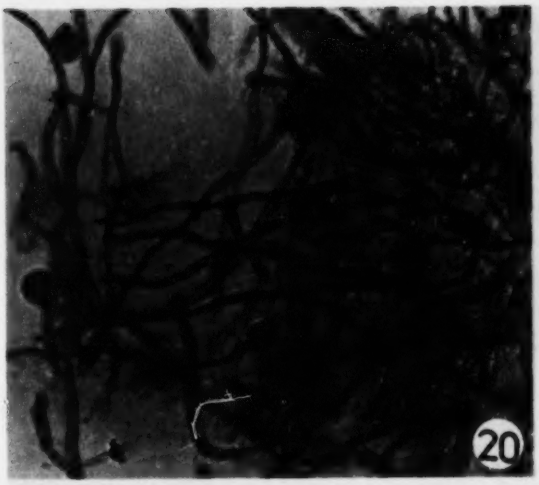
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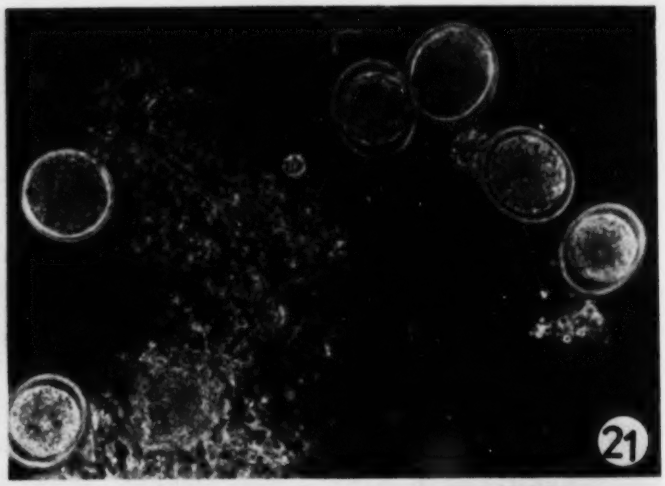
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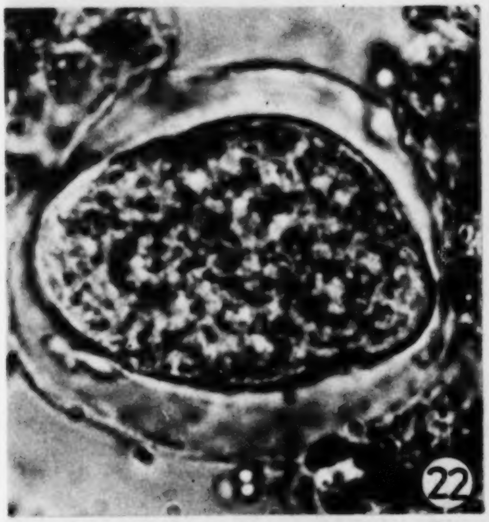
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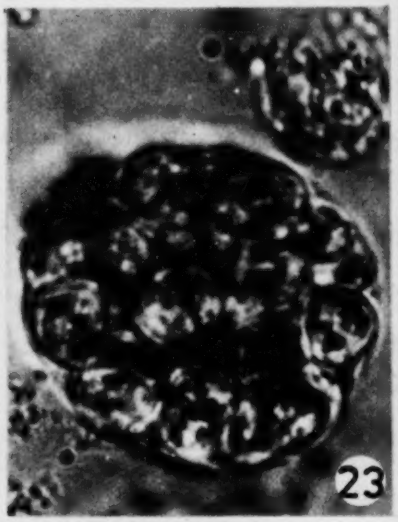
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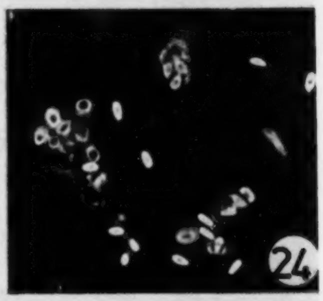
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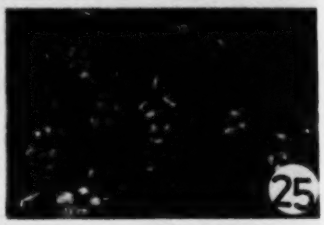
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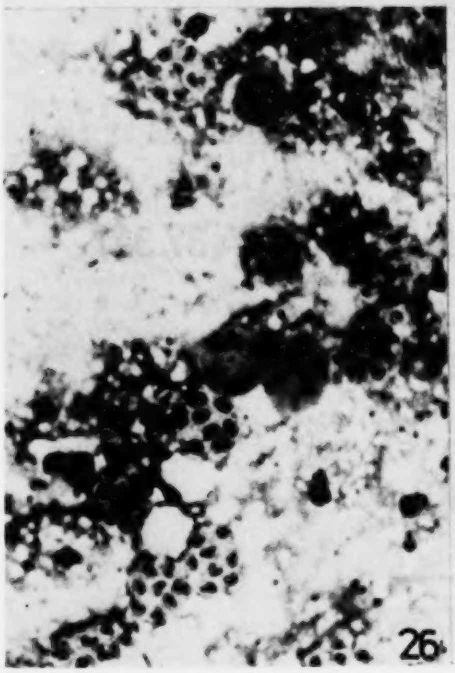
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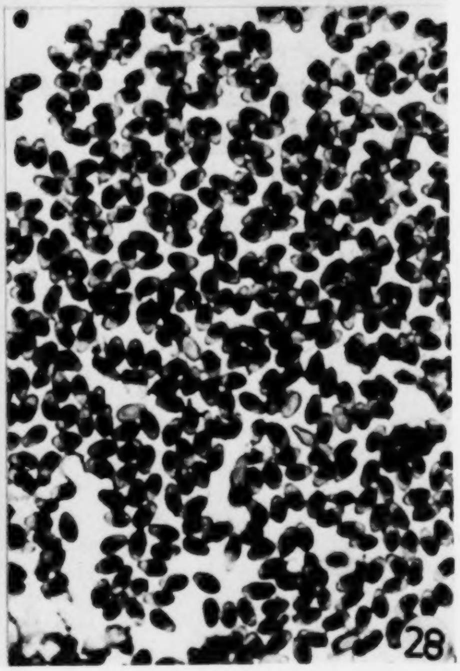
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Figs. 29-38: *DIPTERA* / Figs. 29,30,31, and 33: Heidenhains iron haematoxylin stain; 32,35: fresh condition; 34,39: phaco; 36,37, and 38: Giemsa stain/

29,30. *Helicosporidium parasiticum* of *Ctenosciara hyalipennis*, Different vegetative stages and mature spores in fat body, and intestinale epithelium, 3000 x.

31. *H. parasiticum* of *Ctenosciara spp*., different vegetative stages and mature spores in fat body, and intestinale epithelium, 3000 x.

32,33,34,35. *Ascocystis spp*. of *Megaselia subnitida*, different vegetative stages and spores (oocysts) in ovaries,and eggs.

32. Mature gametocyst with less then 300 oocysts; a. free mature oocysts, 750 x.

33. Mature gametocyst inside of one hosts-egg; a. cyst, b. egg-vitellus, 300 x.

34. Free mature oocysts; a. gamont, 1200 x.

35. Free mature oocysts, 3000 x.

36. *Nosema spp*. of *Platosciarus socialis*, mature spores in fat body, 3000 x.

37. *Nosema spp*. of *Epidapus atomarius*, mature spores in fat body, 3000 x.

38. *Hepatozoon spp*. ? of *Corynoptera spp*., schizonts ? in fat body, 3000 x.

Fig. 39: *COLEOPTERA* / Fig. 39: phaco/

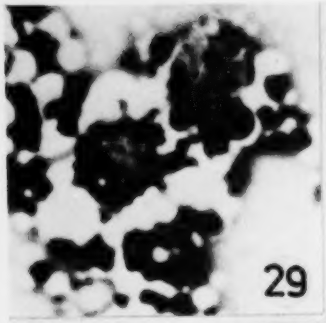
39. *Actinomyxidia* ? in fat body of one larvae of *Coleoptera spp*. 1200 x.

100 m/u (Fig. 29, 30, 31, 35, 36, 37, 38)

200 m/u (Fig. 32)

200 m/u (Fig. 30)

100 m/u (Fig. 34 39)



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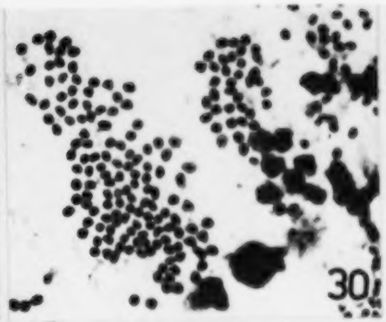

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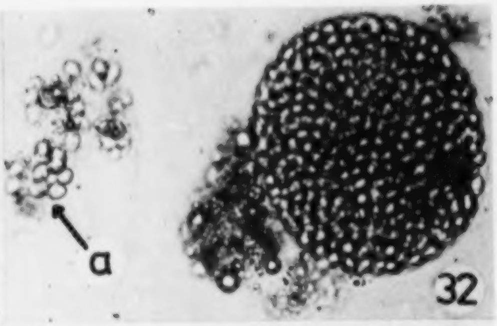

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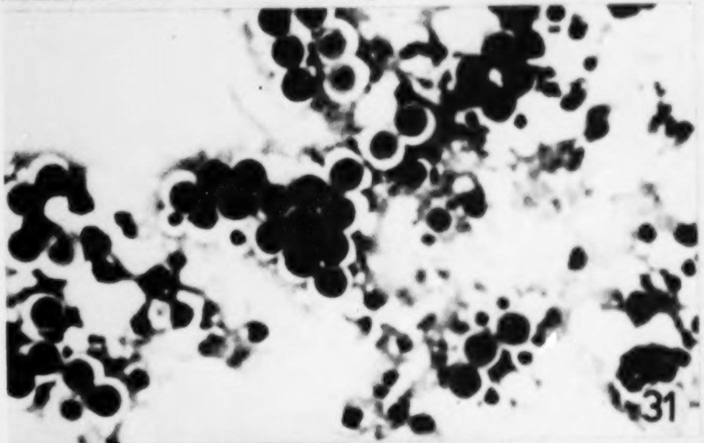

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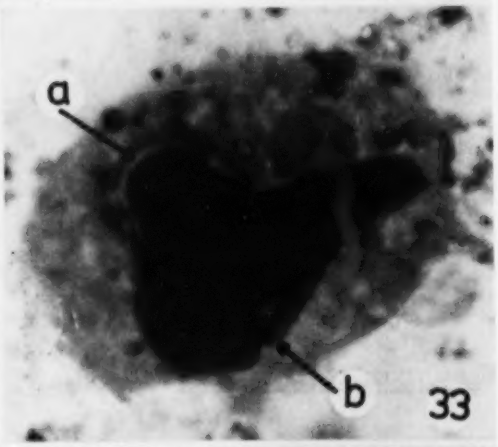

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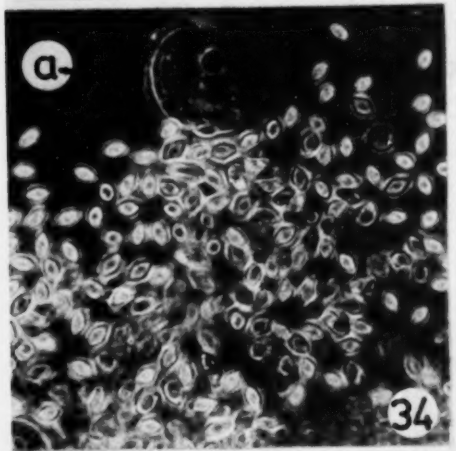

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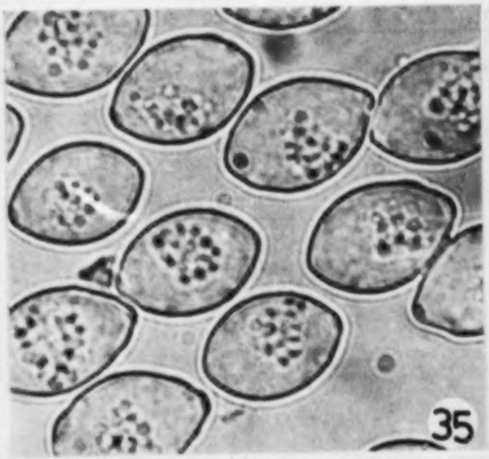

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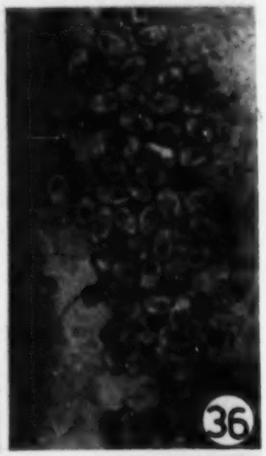

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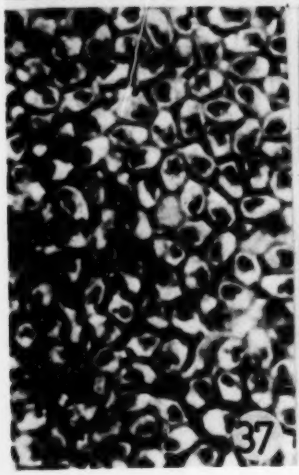

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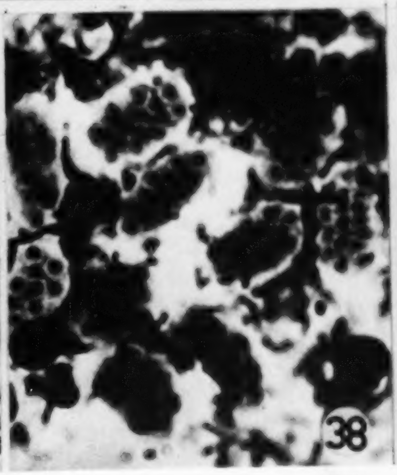

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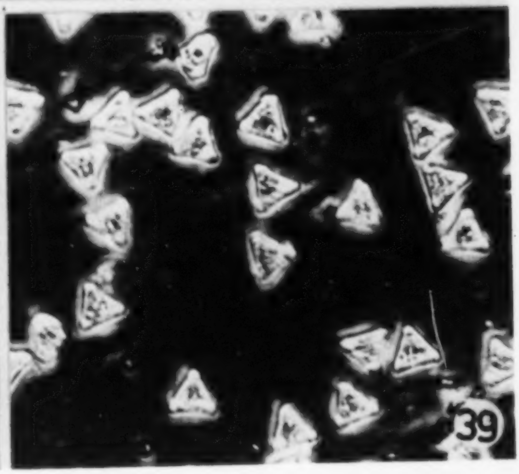

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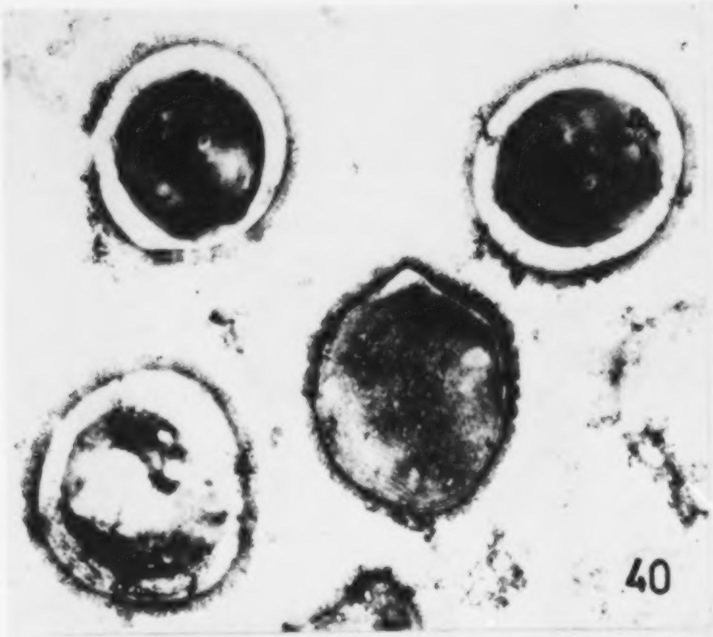
Electron microscopy:

Figs. 40-43: Auraspora gen. nov. of Lepidocyrtus lignorum, the mature spores, Fig. 40: 22000 x, Fig.41: 30000 x. Fig. 42: 60000 x, Fig. 43: 38000 x.



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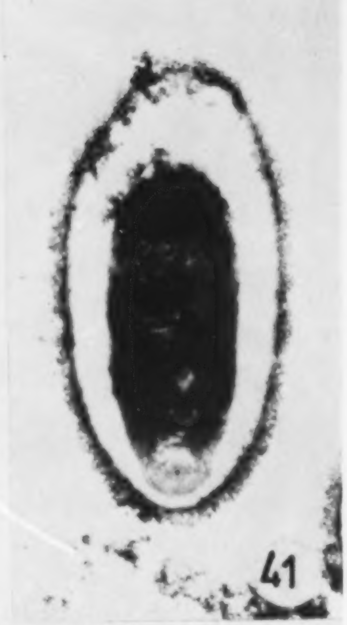

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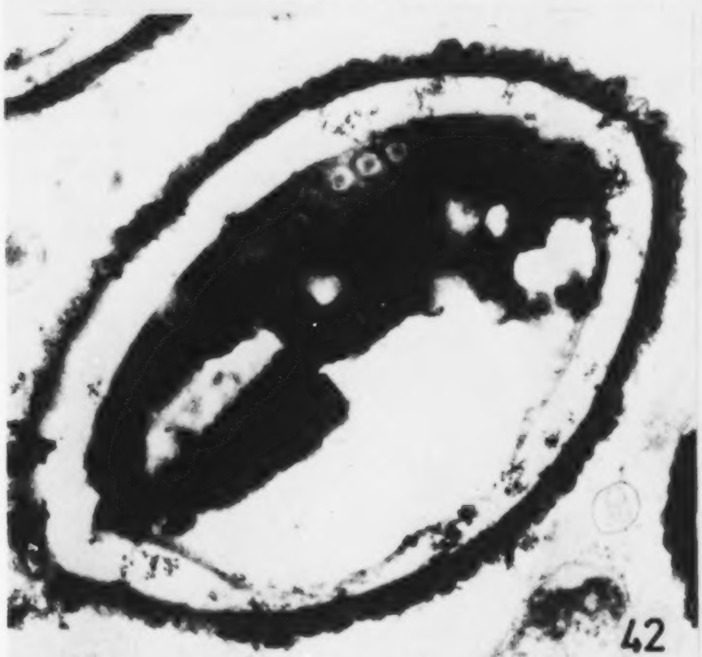

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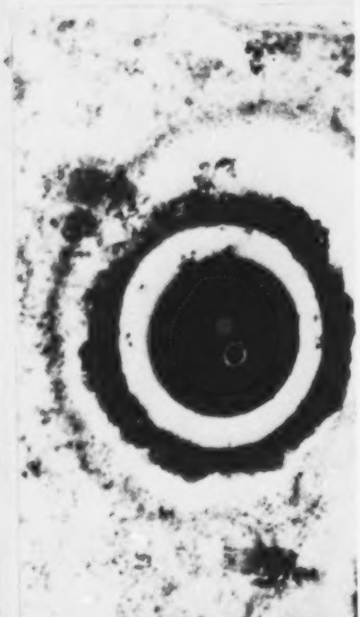
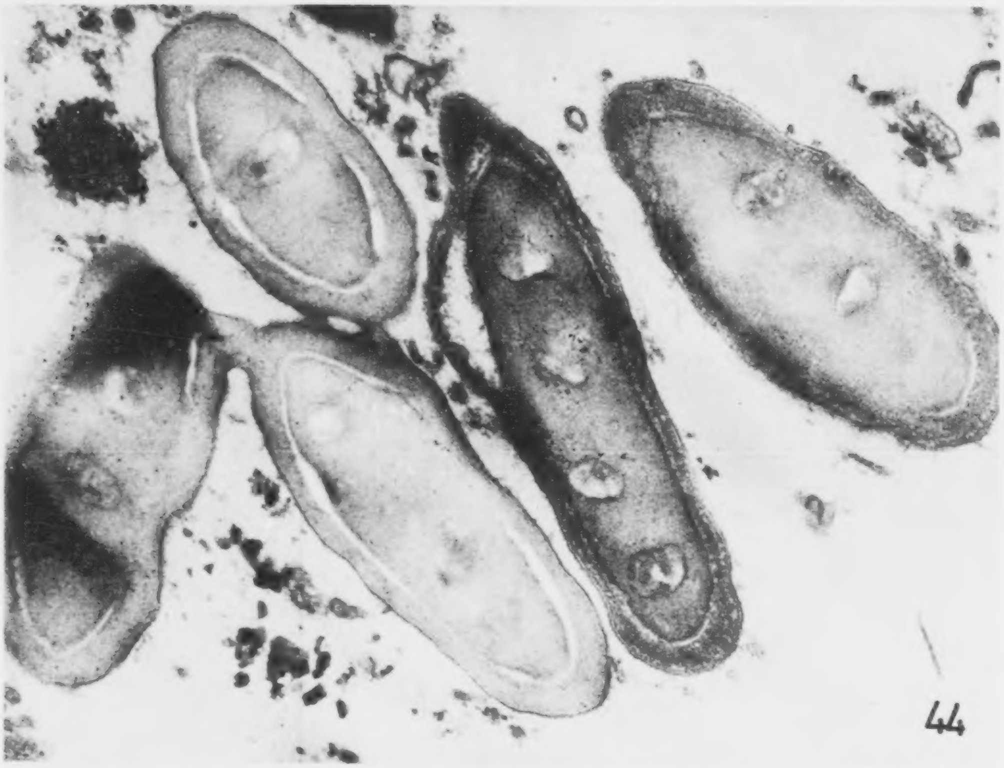


43

Figs. 44,45: *Haplosporidium spp.* ? of *Damaeus clavipes*, the sporogonial stadies of parasite,

Fig. 44: 37000 x., Fig. 45: 38000 x.



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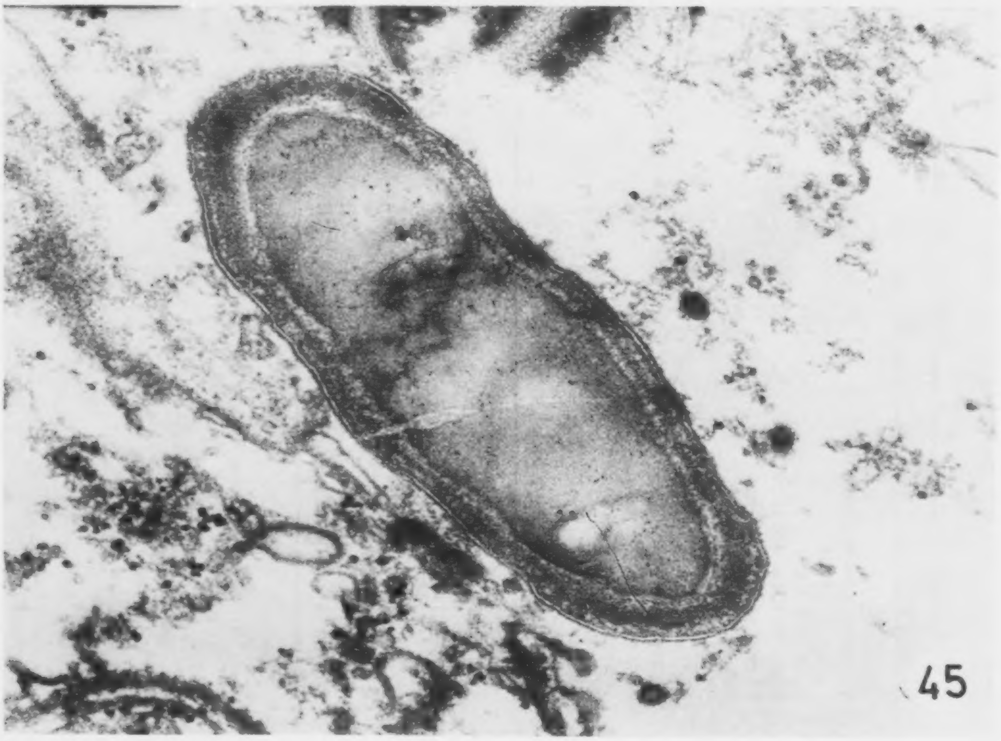

45

Table 4. THE IMPORTANT GENERA OF SPOROZOA (PROTOZOA) OF SOIL DECOMPOSERS FOUND IN FOREST OF LOWER SAXONY, W. GERMANY, 1978 - 1979.

Parasite	TOTAL		EUGREGARINIDA		COCCIDIA	MICROSPORIDA					HAPLOSPORIDA ?
Host	No.Ex.	Inf.%	Mon.	Greg.	Ad.?	Nos.	Pl.	Th.	Enc.	Au.	Hapl.
Oligochaeta	480	36	30	-	-	4	-	-	-	-	-
CRIBATEI:											
Steganacarus magnus	59	20	-	10	-	-	-	-	-	-	10
S. applicatus	242	59	-	21	-	2	-	-	-	-	36
S. striculus	161	61	-	19	-	2	-	-	-	-	39
Rhysotritia duplicata	311	65	-	31	-	-	15	-	-	-	19
Microtritia minima	98	27	-	5	-	6	-	4	-	-	12
Nothrus silvestris	140	45	-	16	-	-	-	-	-	-	29
Platynothrus peltifer	89	26	-	6	-	2	-	-	-	-	18
Damaeus clavipes	412	76	-	26	-	3	-	-	-	-	47
D. onustus	299	57	-	26	-	2	-	-	-	-	29
Cepheus dentatus	83	45	-	25	-	-	5	-	-	-	15
Carabodes coriaceus	91	50	-	21	-	2	2	-	-	-	25
Eupelops hirtus	82	19	-	10	-	2	-	-	-	-	7
Euzetes globulus	112	29	-	10	-	-	-	-	-	-	19
Euphthiracaridae spp.	162	34	-	9	-	-	-	4	-	-	19
COLLEMBOLA:											
Tomocerus flavescens	263	8	-	2	-	-	-	3	2	-	-
Lepidocyrtus lignorum	140	7	-	3	-	2	-	1	-	2	-
L. cyaneus	68	6	-	3	-	3	-	-	-	-	-
Onychiurus quadriocellatus	412	11	-	-	-	11	-	-	-	-	-
O. spectabilis	23	2	-	-	-	2	-	-	-	-	-
Neanura muscorum	97	6	-	-	6	-	-	-	-	-	-
Folsomia quadrioculata	41	2	-	-	-	-	-	2	-	-	-

Legend
No. Ex. = Number examined
Inf. = Infected
Mon. = Monocystis spp.
Greg. = Gregarina spp.
Ad. = Adelina spp. ?
Nos. = Nosema spp.
Pl. = Pleistophora spp.
Th. = Thelohania spp.
Au. = Auraspora gen. nov.
Hapl. = Haplosporidium spp.

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The investigations of parasitic agents in moss-mites have been recorded photographically by us for the first time (Figures 14, 15, 44, 45) a group of microorganisms never seen before (Table 5). The infection was localized in nephrocytes and cells of caecum. However, the morphology and life cycle of this new group of parasites do not suggest a clean systematic status, and we have yet to ascertaim whether these microorganisms belong to Protozoa or Lower Fungi. We consider that these may be close to Sporozoa and the **organisms like** Haplosporida. Detailed light and electron microscopic studies of life cycle and their importance as pathogens of moss-mites are under way. It is hoped that this will help us in deciding more precisely their systematic position. This group of parasites, H. parasiticum, 8 members of Gregarina spp. and 9 species of Microsporida of Oribatei are new.

Of the spring-tails, 9 different microsporidian (Figures 24-28), one coccidian (Adelina spp. ?, Figures 21-23), and one Entomophtorans spp. (Entomophtoraceae, Fungi) parasites were found during our investigation. Of microsporidian parasites, three were belonging to the genus Thelohania, 4 to genus Nosema, while one was close to the definition of the genus Encephalitozoon (or Perezia of the recent revision of French authors)and one belongs to a genus Auraspora gen. nov. (Figures 23, 4-, 41, 42, 43) which is not yet included in the system of Microsporida. All the discovered species of parasites in Collembola are also new.

It is evident that soil fauna other than those reported then were also infected by different parasites. Intensive studies have been carried on the parasites of dipterans and coleopterans. Of 340 specimens of dipterans inspected, the infections rate was 16% (10% Fungi, 2% Rhizopoda, and 4% Sporozoa). The most important parasites were as follows: Helicosporidium parasiticum found in Ctenosciara hyalipennis Meigen (Fam. Sciaridae, Figures 29-31); Sporozoa of the genus Ascocystis (Lecudinidae, Eugregarinida) in Megaselia subnitida Lundbeck (Fam. Phoridae, Figures 33-35), and two Nosema spp. (Microsporidia) in Platosciara socialis Winnertz and Epidapus atomarius Degeer (Fam. Sciaridae, Figures 36, 37), and perhaps the genus Hepatozoon ? (Sporozoa, Coccida , Figure 38). The questionable genus Hepatozoon (?) was found in one dipteran of Corynoptera spp. (Fam. Sciaridae). In Coleptera the infection rate was 22% (2% Nematodes, 17% Fungi, and 3% Sporozoa) in samples of 560 specimens examined. The most interesting parasites of Coleptera were the group of Sporozoa: Actinomyxidia (?) found in one host larvae (Figure 39). This group of parasites found in Coleoptera is very unusual for insects as hosts. The infection levels of Orthoptera, Rhychota, Hymenoptera, and Lepidoptera are presented in Table 1 and 2. No infections was recorded in the Myriaopoda.

CONCLUSIONS

Studies on the parasites of soil fauna in mixed coniferous forests, mixed leaf forests, and pure beech forests of Lower Saxony, W. Germany reveal that:

1. Of all soil fauna (8478 specimens) examined, the highest level of infection was found in the animals of mixed deciduous forests (average level 12%), followed by pure beech forests (6%), and mixed coniferous forests (3%).

2. The population densities of soil decomposer fauna in the forests surveyed were regulated by the Nematoda, and four groups of microorganisms, namely; Viruses, Bacteria, Fungi, and Protozoa.

3. Of total percentage of infection of decomposers, the highest level was shown by Oligochaeta (54%), Acarina (42%), and Apterygota (7%).

4. Of parasites, the most important group of pathogenic agents were Sporozoa (Protozoa) and Fungi.

5. Sporozoa (Protozoa) infecting the decomposers were studied and identified to the family, genus or species level. This revealed a large number of new species belonging to: Microsporida , Coccida , Gregarinida and possibly Actinomyxidia, and Haplosporida .

6. These studies also revealed one unknown group of microorganisms which infected 15 species of moss-mites (Oribatei, Acarina). Detailed studies of their life cycle are under way.

7. The establishment of Helicosporidium parasiticum Keilin, in different species of Euphtiracarus spp. (Euphtiracaridae) and in Ctenosciara hyalipennis (Sciaridae, Diptera) represent also a very important feature for the pathology of these Arthropoda.

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QUESTIONS and COMMENTS

C.A. EDWARDS: Did you investigate the pathogens of nematodes?

K. PURRINI: No, we didn't.

E. WALDORF: Would you speculate on the differences in incidence between Collembola and Acari?

K. PURRINI: Yes, there are big differences. The acarines are not very resistant against the diseases. In Lower Saxony (West Germany) the level of infections in acarines was 62%; in Collembola only 7%.

C. EASTMAN: Will you or your Institute colleagues be looking at virus infections in soil arthropods?

K. PURRINI: Yes, we will be looking at virus infections. I've just found two viral diseases, one in *N. muscorum* (Collembola), and one in the larvae of *Cantharus* sp. (Fam. Cantharidae, Coleoptera).

INTERACTIONS BETWEEN NEMATODES AND BACTERIA IN HETEROTROPHIC SYSTEMS WITH EMPHASIS ON SEWAGE SLUDGE AND SLUDGE AMENDED SOILS

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The high densities of free-living nematodes in a wide variety of ecosystems has long prompted interest in their functional role. Since bacteria appear to be responsible for only a minor fraction of nutrient regeneration in marine systems (Johannes, 1968), faunal grazing has been considered to be a major decomposition pathway. Therefore, by virtue of their high density and elevated metabolic rate, nematodes have been considered important with regard to nutrient cycling and energy flux by workers on marine benthos (Johannes, 1965; Tietjen, 1967; Tietjen et al., 1970; Gerlach, 1971).

In contrast, terrestrial ecologists have stressed the dominance of bacteria and fungi as well as the subservience of the microfauna and mesofauna in decomposition processes. Therefore, investigations of the ecological importance of terrestrial nematodes have largely overlooked their possible role in decomposition and have instead concentrated on their population dynamics and their contribution to total community biomass and respiration. However, previous workers have demonstrated that invertebrates play a role far more significant than their biomass or population metabolism would indicate by their stimulation of microbial populations and hence alteration of decomposition rates of various organic substrates (Hinshelwood, 1951; MacFadyen, 1961, 1963; Heath, Edwards and Arnold, 1964; Johannes, 1965; Stout, 1973, 1974; Fenchel and Harrison, 1976; Mitchell, 1978, 1979). Our previous work has demonstrated that bacterial feeding nematodes, specifically Pelodera punctata (Cobb), stimulate bacterial population growth and activity and thus have an accelerating effect upon sewage sludge decomposition (Mitchell, Hornor and Abrams, 1980; Abrams and Mitchell, in rev.).

The purpose of this paper is to present and compare our findings with those from other investigations so that a more complete understanding of the role of nematode-bacterial interactions in heterotrophic systems may be ascertained. Specific emphasis will also be placed on the investigations of Anderson and Coleman (1977), Anderson et al. (1978) and Coleman et al. (1978), since these latter studies are the only ones presently available which are comparable to our work.

Nematode population metabolism and biomass in various habitats

Nematode abundance, biomass and respiration data, which were obtained from various sources, are presented in Table 1. Several investigators have estimated the contribution of nematodes to total soil metabolism. It is evident that in those habitats dominated by plant

TABLE 1. NEMATODE DENSITY, BIOMASS AND POPULATION METABOLISM IN VARIOUS HABITATS.

Habitat	Nematode Densities (individuals m^{-2})	Nematode Biomass ($g\ m^{-2}$)	Population Metabolism ($ul\ O_2\ m^{-2}\ H^{-1}$	Temperature (°C)	Dominant Feeding Group	% Contribution to Total Faunal Metabolism	Authority
Moorland Soil	$3.06 x 10^6$	0.75	$4.9 x 10^2$	16	Plant Feeders	.6	Banage, 1963
Grassland	$1.70 x 10^7$	10.5	$1.1 x 10^3$	16	Plant Feeders	16	Nielsen, 1949 MacFadyen, 1963
Beech Forest	$1.09 x 10^6$	0.28	$2.4 x 10^2$	16	Plant Feeders	5	Yeates, 1972 Phillipson et al., 1977
Subarctic Tundra	$3.56 x 10^6$	2.64	$8.0 x 10^3$	--	Bacterial Feeders	75	Kuzmin, 1976
Marine (Salt Marsh)	$2.10 x 10^6$	18.4	$1.8 x 10^5$	20	Microbial Feeders	33	Wieser & Kanwisher, 1961
Sewage Sludge	$1.40 x 10^7$	2.80	$5.0 x 10^4$	22	Bacterial Feeders	67	Mitchell et al., 1978 Abrams & Mitchell, in rev., Unpublished data

(macrophyte) feeding nematodes, they contribute a relatively small proportion of the total soil metabolism. Examples of such systems include bog or moorland soils where the acidity precludes high densities of bacteria and thus plant and fungal feeding nematodes dominate (Banage, 1963).

The abundance of herbaceous material in grasslands also tends to favor plant feeding nematodes. However, Twinn (1974) noted that population densities of bacterial feeding nematodes varies considerably in grasslands and they sometimes compose up to 50% of the total nematode fauna. This variation has been attributed, in part, to the spatial arrangement of vegetation. Hence, selection of certain samples in accordance with vegetation location may bias density estimates toward plant feeding nematodes and overlook the contribution of bacterial feeders which would be found in more open areas (Twinn, 1974).

In deciduous forests, such as the beech mull studied by Yeates (1972) and Phillipson et al. (1977), the wide variety of food resources allows nematodes to be distributed throughout various trophic groups. In addition, the favorable soil conditions in such habitats permit a wide variety of organisms, including bacteriophagous macrofauna to flourish. Therefore, the relative contribution of nematodes to total soil metabolism may be less.

It is in more severe environments that the importance of nematodes becomes most evident. In spite of the relatively low pH of 5 in the subarctic tundra site which was studied by Kuzmin (1976), bacteria were far more abundant than fungi (Chernov et al., 1975). Hence, bacterial feeding nematodes were dominant over plant and fungal feeders. Kuzmin (1976) also noted that although nematodes comprised only 30% of the biomass in some sites, they were responsible for up to 75% of the total faunal metabolism.

In both marine sediments and sewage sludge the ability of nematodes to survive anoxic conditions permits them to be active in habitats where other fauna are excluded. Oxygen depletion may occur in estuarine environments, where microbial activity is considerable as well as in profundal sediments (Weiser and Kanwisher, 1961). As an adaptation to these low oxygen tensions, some marine species, such as Enoplus brevis (Bastian) possess oxyhaemoglobin to regulate oxygen supply to various tissues as well as store oxygen when it is present in low concentrations (Atkinson, 1975). Similarly, P. punctata, the dominant species in an activated sludge, is also able to survive anoxic conditions and be active under low (pO_2 7000 dyne cm^{-2}) oxygen tensions (Abrams and Mitchell, 1978). This is especially critical in the early stages of sludge decomposition, when anaerobic processes may predominate and oxygen depletion occurs (Mitchell, Hornor and Abrams, in rev.).

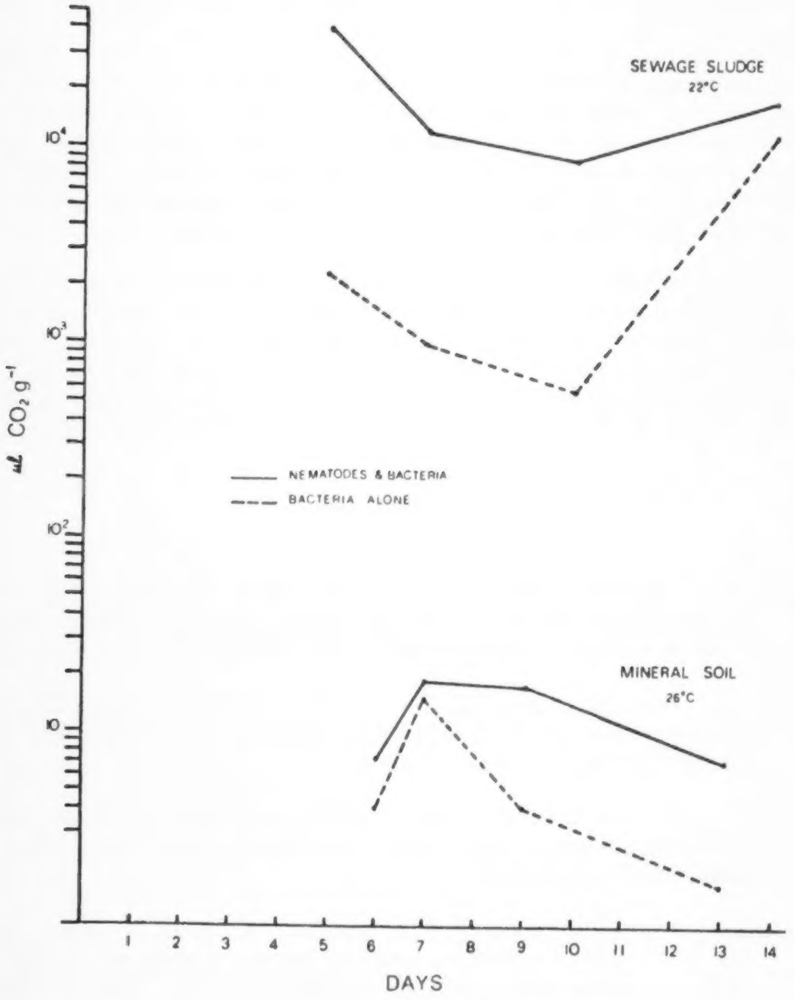
The importance of nematode-bacterial interactions on substrate metabolism

A field study of sewage sludge in drying beds revealed high densities of P. punctata and other bacterial feeding rhabditid nematodes when decomposition, as indexed by oxygen consumption and methand evolution was proceeding rapidly (Mitchell et al., in rev.). Similarly, in a study of the effects of sludge addition to a silt loam topsoil, nematode densities increased, then decreased with time in correspondence with organic matter catabolism (Mitchell et al., 1978). Studies of nematode-bacterial interactions in glass bead microcosms have demonstrated that bacterial activity, which was reflected in oxygen consumption and carbon dioxide evolution is significantly increased in the presence of nematode grazing (Anderson and Coleman, 1977; Mitchell et al., 1980). In addition, bacterial population densities were also significantly ($p < 0.05$) increased by nematodes (Mitchell et al., 1980). Studies in sterilized sludge microcosms yielded similar results. The feeding activities of rhabditid nematodes (*P. punctata*) stimulated microbial (*Pseudomonas fluorescens*) metabolism as was reflected in significantly ($p < 0.01$) increased oxygen consumption and bacterial densities (Abrams and Mitchell, in rev.). In addition, nematode movement also helped to distribute *Ps. fluorescens* within the sludge. Organic matter losses were found to be twice as great over 35 days in microcosms containing nematodes and bacteria than in those containing bacteria alone (Abrams and Mitchell, in rev.).

While this effect is of major importance in substrates with a high organic matter content, it may not be as pronounced in mineral soils where food resources are more limiting. In microcosms containing sterilized mineral soil, Anderson et al. (1978) noted that bacterial densities were slightly higher after 17 days of nematode feeding but after 24 days were significantly ($p < 0.05$) reduced. However, the metabolic activity of the mineral soil microcosms was only a fraction of that observed in the sludge microcosms. Even after substantial (600 ppm) glucose amendments, bacterial densities did not exceed 10^9 individuals g^{-1} dry weight in the mineral soil throughout the 24 day study (Anderson et al., 1978). In contrast, bacterial densities (inoculated at the same order of magnitude) in the sludge microcosms were as high as 10^{11} individuals g^{-1} after 5 days. Assuming a respiratory quotient (R.Q.) of 1.00 for carbohydrate catabolism, the data of Coleman et al. (1978) for mineral soil can be compared with the sludge respiration data (Figure 1). Carbon dioxide evolution in the sludge microcosms over 14 days was more than 600 times greater than that of the mineral soil microcosms. Although the organic matter content of the mineral soil, with glucose additions was no more than one sixth of that in sludge, losses over 35 days would only amount to 0.00347% of the organic matter as opposed to 6.89% in the sludge microcosms for the same time period. In the absence of nematodes, organic matter losses would be .00015% and 3.51% for the mineral soil and sludge microcosms, respectively.

The data support the hypothesis that nematodes have an accelerating effect upon decomposition, and that this effect is of greater significance in substrates high in organic matter. In such substrates, food resources may not be as limiting and, hence reproduction of bacteria may be rapid and continuous. Predation by nematodes keeps bacterial populations actively growing and distributed throughout the

FIGURE 1. Comparison of sewage sludge (Abrams and Mitchell, in rev.) and mineral soil (Coleman et al., 1978) catabolism in the presence and absence of bacterial feeding nematodes.



material. In substrates where organic matter is less abundant, predation by nematodes accelerates the natural decline of microbial populations which accompanies the depletion of the food resources.

Directions for future research

More direct observations of the feeding habits of soil nematodes are needed. Previous studies have been based largely on gut content analyses or buccal cavity shape. Gut content analyses may be somewhat inaccurate since often, only hard, indigestible items are recognizable (McIntyre, 1969; Tietjen, 1969; Tietjen and Lee, 1977). In addition, bacteria and other small organisms may be taken in with larger food items, causing discrepancy as to the predatory nature of some species. Buccal cavity shape may be misleading as well, since different types of buccal cavities may be correlated with other physiological functions, such as oxygen uptake (Wieser and Kanwisher, 1961). In addition, stomal shape may be indicative of the size classes of food items, not necessarily the biological origin of those items.

The effects of bacterial feeding nematodes on soil processes such as carbon flux and mineralization should be explored further. In addition, the relationships among nematodes and other soil organisms should be investigated. Emphasis on microfloral-faunal interactions, rather than compartmentalization of specific taxa would enhance our understanding of decomposition processes within heterotrophic systems.

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QUESTIONS and COMMENTS

D. COLEMAN: Did you determine the fraction of the total organic carbon which was soluble?

If this was high (perhaps ½ of your total of 60% organic matter) that would account for your very high microbial activity.

B.I. ABRAMS: This sludge contains a high percentage of labile carbon compounds and hence its decomposition rate is extremely rapid. More information on the chemical composition and decomposition rate of this sludge has been presented in Mitchell et al. (1978), which is referenced in our paper.

S. HILL: Do you consider that nematode movement is important, in addition to feeding, in their promotion of bacterial activity?

B.I. ABRAMS: Their movement through the substrate does create additional surface area and micropore space and also distributes bacteria within the substrate. However, where this effect is active and of a mechanical nature in the case of larger invertebrates, it is passive in the case of nematodes since they move in an aqueous film.

USE OF MICROARTHROPODS (MITES AND SPRINGTAILS) AS VALUABLE INDICATORS OF SOIL METABOLIC ACTIVITY

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France

ABSTRACT

It is well known that most of the metabolic activity in soil is due to microbial activity. Accordingly, overall soil respirometry or microbial counts are often used as an indicator of soil metabolism. Because conflicting results are often obtained, soil fauna is not yet considered as a reliable indicator for this purpose. In this paper we have tried to determine whether soil fauna can be used as a valuable indicator of soil metabolic activity.

Soil cores from two forest soil types (a rendzine or calcareous soil, pH8.5, and a podzol or loamy sandy soil, pH 3.7) were desiccated or sterilised by heat (30°C, 60°C, 105°C, 200°C) then replaced in the field, to allow invasion by Microarthropods and Microorganisms from surrounding soil. Respirometric activity was measured weekly in treated and undisturbed soil core samples during a one month incubation period. At both sampling sites, qualitative and quantitative variations of bacteria and fungi were carried out, and invasion by Mites and Collembola were checked weekly. Soil respiration rates and microbial counts were much higher in calcareous soil cores than in those of loamy sandy soil. Colonization by Collembola was significantly more intense than by Oribatid Mites in alkaline soil cores, but in acid soil an opposite pattern was observed. These preliminary results indicate that it may be possible to characterize soil biological activity by Microarthropods invasion, related to relatively fast microbial growth, enhanced by previous desiccation of soil cores.

RESUME

Tous les spécialistes du sol s'accordent à déclarer que l'activité métabolique d'un sol est principalement dûe au développement de la microflore tellurique. En conséquence, les mesures respirométriques du sol et les énumérations de germes constituent d'excellents indicateurs de l'activité métabolique totale du sol. Parce que de

nombreux résultats contradictoires ont été souvent obtenus la faune su sol ne peut être encore considérée comme un indicateur sûr du métabolisme du sol. Dans cet article, nous proposons une méthodologie nouvelle permettant d'utiliser les microarthropodes du sol comme estimateurs de l'activité métabolique du sol.

Des échantillons de terre provenant de deux types de sol (rendzine pH = 8,5 et podzol pH = 3,7) ont été desséchés ou stérilisés à la chaleur (30°C, 60°C, 105°C et 200°C), puis réintroduits à leur emplacement dans le terrain de manière à permettre le libre retour des Microarthropodes et des Microorganismes. Des mesures d'activité respiratoire ont été effectuées chaque semaine pendant un mois sur les échantillons traités et témoins, ainsi que des estimations qualitatives et quantitatives des germes bactériens et fongiques. Simultanément et respectant la même périodicité, le retour des Acariens et des Collemboles a pu être contrôlé.

Les consommations d'oxygène et les énumérations de germes ont été plus élevées dans le sol calcaire que dans le sol limoneux. De même, la colonisation par les Collemboles a été beaucoup plus intense que celle des Acariens dans le sol alcalin, alors que le processus est inverse dans le sol acide. L'ensemble de ces résultats démontre qu'il est possible de caractériser l'activité biologique d'un sol par le taux de colonisation des Microarthropodes provoqué par une relance de l'activité microbiologique dans des échantillons de sol préalablement desséchés, puis réintroduits _in situ_.

INTRODUCTION

Most of the metabolic activity in soil is due to microbial activity and soil biologists generally admit that animal metabolism accounts for only 10 per cent of the total soil metabolism (MACFADYEN 1968). CROSSLEY (1977) reports that some recent studies have estimated that soil fauna contributes less than 1% to the annual average CO_2 production from forest soils. Accordingly some authors have attributed indirect regulation, through microfloral-faunal interactions, as playing a major role for soil arthropods. It is a common finding that in animal sampling some soil samples contain low counts of all species while others may contain many abundant species although soil respiration values remain very uniform. Because conflicting results are often obtained, soil fauna is not yet considered as a reliable indicator of soil metabolism. Under these conditions, most studies of soil metabolism mainly concern microbial activity and have used evolution of CO_2 production

over time as an indicator of overall respirometry activity (COLEMAN, 1973).

To remove any uncertainty about the use of soil fauna as an objective tool for estimating soil metabolic activity, we have attempted a new approach based on the recolonisation by microarthropods in heat desiccated soil samples, maintained in the laboratory, then replaced in the field.Little is known about how quickly and by what route treated soil becomes recolonised. The recolonisation of sterilised soil by soil arthropods was previously studied by BUAHIN (1965) who showed that soil sterilised by chemicals was recolonised by all arthropods more slowly than soil sterilised by heat.

This paper reports results which are partly drawn from a previous work on relationships between soil fauna and soil microflora (KILBERTUS, VANNIER, VERDIER, 1976).

METHODS

Two types of forest soil were used for comparison. At Brunoy, South of Paris, an alkaline soil or brown calcareous soil in Hornbeam wood (pH 7.5-8.5 ; C/N 10-12), and an acid soil or sandy loam soil in Oak forest (pH 3.7-4.4; C/N 23-30).

In each forest site within a five square meters area and at the same time in spring 1975 (12th May - 9th June), were cored 96 soil samples (5cm deep, 20 cm^2 area), brought into the laboratory, desiccated at different temperatures (30°C, 60°C, 105°C, 200°C), then replaced in the field to allow invasion by microarthropods and microorganisms from surrounding soil. All these treated soil samples were free of any arthropods and those heated at high temperatures (105°C, 200°C) were totally sterilised.

After one week of incubation in the field, six soil samples of each treatment, plus six of undisturbed soil were removed weekly during one month, and used for respirometry measurements in an incubator, counts of microbial germs on gelose culture, and microarthropods extractions by a dry funnel system.

In addition, soil moisture was controlled in each site at the same time. After only one week of natural incubation, all treated soil samples restablished their optimal moisture content compared with the surrounding soil.

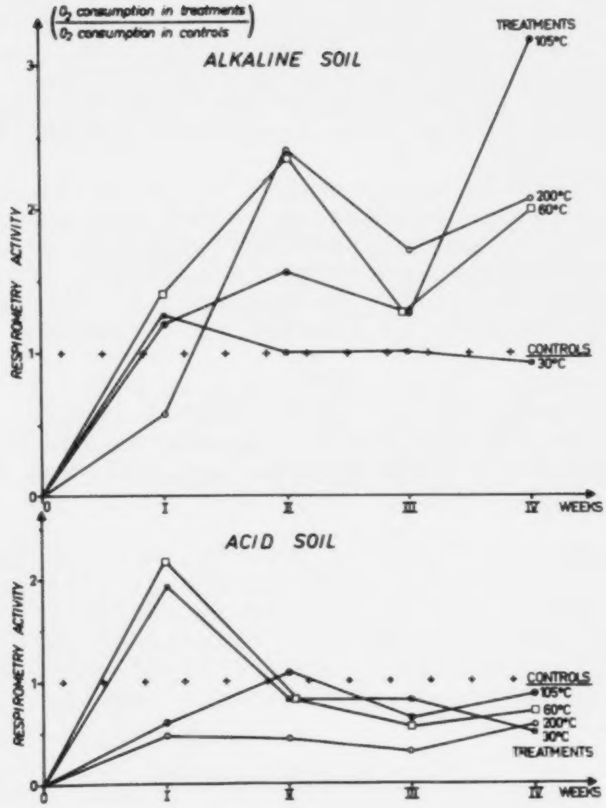


Figure 1. - Weekly respirometry activity in heat desiccated soil samples then replaced in the field, and in controls.

RESPIROMETRY ACTIVITY

Each soil sample used for respirometry activity was placed in a small chamber or incubator from which a small volume of gas was removed after two hours incubation, then analysed with a Scholander 0.5 cc. gas analyser, as described in VERDIER (1975). Respirometry activity is best charactarized by the oxygen consumption rather than by the CO_2 production, in the case of alkaline soil because of the combination of CO_2 with carbonates (VERDIER, 1975).

In figure 1, respirometry activity is expressed as a ratio between O_2 consumption in treated soil samples and O_2 consumption in undisturbed soil samples or controls. The level of respirometry activity in controls indicates the line of reference (+1) to be compared to the levels of respirometry activity in treated soil samples.

In alkaline soil, soil samples initially heated at high temperatures (60°C, 105°C, 200°C) showed a peak of activity after two weeks and a second increase two weeks later. Conversely a low response was recorded in the case of soil dried at 30°C.

In acid soil samples, results were quite different : respirometry activity in soil heated at high temperatures (105°C and 200°C) did not attain the level of natural soil activity. In the cases of soil treated at 30°C and 60°C, after a short increase during the first week, the respirometry activity dropped under control levels.

MICROBIAL COUNTS

Microbial counts have been made on agar-agar culture using the method described by REISINGER and KILBERTUS (1975).

Desiccation always promotes growth of a limited species of germs, but in large quantities, at the expense of total microflora. Table 1 shows the same phenomenon in all treated soil samples of alkaline soil except for the treatment at 30°C. Drying by heat followed by natural rehydration caused the development of an overwhelming number of microorganisms where Actinomycetes dominated ; for instance 597,000 10^3 germs per gramme of dry soil in treated soil samples at 105°C versus 3,668 10^3 germs per gramme of dry soil in control soil samples. A restricted number of fungi species were found, only five at 30°C, six at 60°C, none at 105°C and 200°C while normally twenty-two species occur in untreated soil.

Table I. - WEEKLY COUNTS OF GERMS (x 10^3) PER GRAMME OF DRY SOIL IN HEAT DESICCATED SOIL SAMPLES THEN RE PLACED IN THE FIELD, AND IN CONTROLS.

ALKALINE SOIL

WEEKS TREATMENTS	FIRST	SECOND	THIRD	FOURTH
at 30°C	35,320	25,700	21,200	52,500
at 60°C	74,430	255,000	339,000	223,000
at 105°C	130,960	453,000	597,000	264,000
at 200°C	81,150	148,000	72,200	106,000
CONTROLS	19,090	19,700	3,668	13,800

ACID SOIL

WEEKS TREATMENTS	FIRST	SECOND	THIRD	FOURTH
at 30°C	78,75	12,550	14,400	3,200
at 60°C	45,840	40,800	9,000	25,400
at 105°C	8,302	20,400	42,600	29,100
at 200°C	32,800	40,800	85,000	92,800
CONTROLS	5,415	15,900	2,990	3,400

In acid soil, microorganisms are less abundant than in alkaline soil and differ by the lack of Actinomycetes which are replaced by Bacillus and Arthrobacter. Counts concerning acid soil samples are not very high (Table 1) reflecting a lower microbial activity than in treated alkaline soil samples. These results corroborate those recorded previously in soil respirometry study (Fig. 1).

ASSESSMENT OF MICROARTHROPODS

Invasion by mites (Oribatei, Mesostigmata) and springtails (Isotomidae and Entomobryidae) was compared in each type of soil at the same temperature treatments (Fig. 2 and 3). Relative frequencies were expressed as a ratio between the number of individuals extracted from treated soil samples and the number of individuals extracted from undisturbed soil samples (controls), so that the reference line (+1) represents the animals identified in the control soil samples.

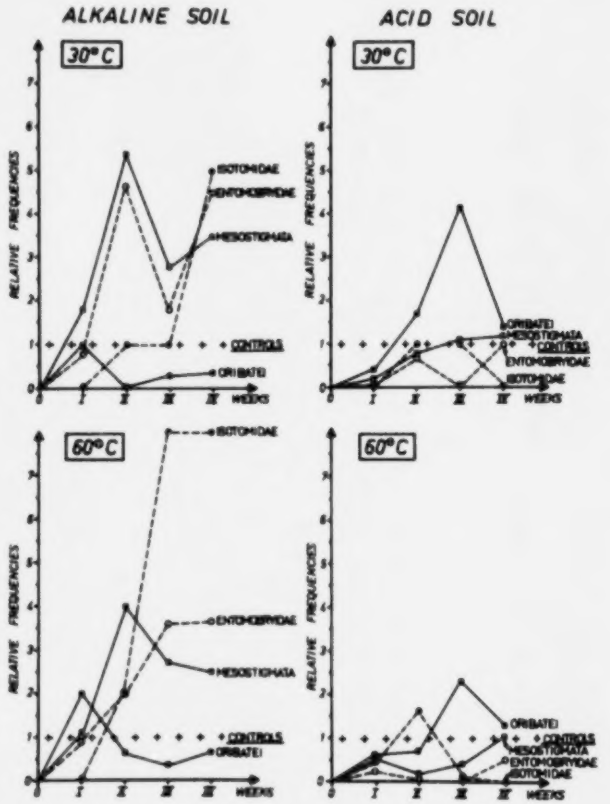
In alkaline soil, at 30°C, Isotomidae and Entomobryidae rapidly invaded the treated soil samples as compared to those found in untreated soil samples (controls). Oribatid mites, on the contrary, did not reinvade on these treated soil samples.

The same pattern was evident at other temperature treatments (Fig. 2 and 3). Recolonisation by Collembola was always more intense than by Oribatid mites ; for instance at 105°C and on fourth week of incubation, Isotomidae were eight times as abundant in control soil samples and Entomobryidae were 5.5 times more abundant, while a half of the Oribatid populations were collected in the same treated soil samples. At 200°C, the numbers of Isotomidae and Entomobryidae greatly diminished in treated soil samples but still exceeded those in undisturbed soil samples.

In acid soil at any temperature treatment an opposite pattern was recorded. Oribatid mites were commonly collected and their numbers always exceeded the populations in undisturbed soil, while the Collembola populations in the same treated soil samples were lower than in controls. At 30°C, 60°C, 105°C and 200°C temperature treatments, Oribatid mites were respectively 4.2, 2.3, 6.2 and 2.2 times as abundant as in controls after three weeks of incubation.

A crossed experimental paradigm was performed in December 1975 in the same sites where desiccated acid soil samples at 105°C were placed in alkaline soil area, and desiccated alkaline soil samples were introduced in acid

Figure 2. - Recolonisation of heat desiccated soil samples (30°C and 60°C) by mites and springtails as compared to controls in two types of forest soil.



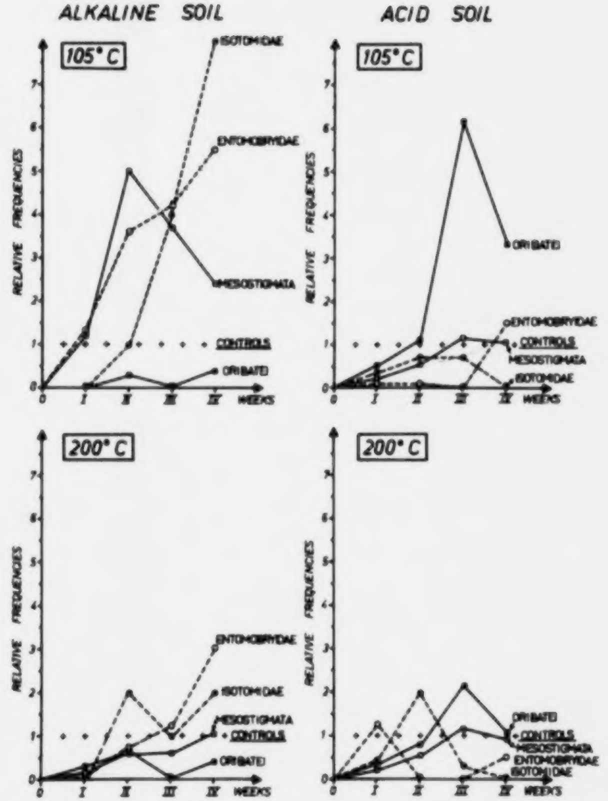


Figure 3. - Recolonisation of heat desiccated soil samples (105°C and 200°C) by mites and springtails as compared to controls in two types of forest soil.

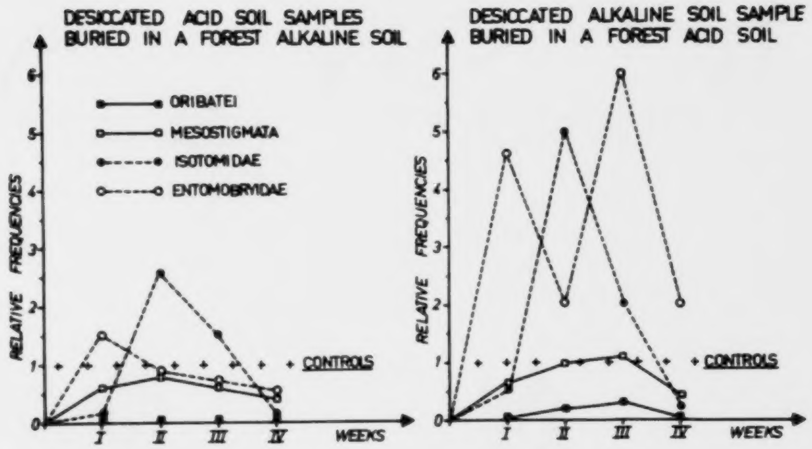


Figure 4. - Crossed experimental model showing the specifity of recolonisation pattern in heat desiccated soil samples.

soil area. Figure 4 summarizes the results :

- in alkaline soil area, treated acid soil samples retained the typical pattern of an acid soil, with a low rate of recolonisation by Collembola, with however an absence of Oribatid mites.
- in acid soil area, treated alkaline soil samples maintained the specific pattern of an alkaline soil with a high increase of Collembola (Isotomidae and Entomobryidae), and much less Oribatid mites than in controls.

All these results tend to confirm the specificity of the process of recolonisation by microarthropods towards the overall activity in a forest soil.

CONCLUSION

These preliminary findings indicate that it may be possible to distinguish soils with a high metabolic activity from soils with low metabolic activity, using a process of recolonisation by soil animals into desiccated soil samples. It is not necessary to establish a statistical analysis to demonstrate that the colonisation by microarthropods is influenced by a fast microbial growth enhanced by previous desiccation of soil samples.

This method may be useful since little work is involved, and only limited knowledge of soil biology is required. The procedure is simple and merely involves collection of soil samples from the field, desiccation in an oven at 60°C or 105°C over 48 or 24 hours, replacement of the samples in the field, then after one week, the extraction of soil fauna from experimental and controlled soil samples. In case of loose ground, small cylindrical baskets made of wire gauze sieve (mesh 2 mm) were used, filled with heat desiccated soil, then introduced in field. This procedure makes easier the removal of treated samples.

In addition, desiccated soil samples incubating in natural soil provides a substrate to which a great number of soil animals are attracted only one week later. For instance, we have collected 96 Lepidocyrtus lanuginosus (Collembola Entomobryidae) in one treated soil sample (100 cc. volume) as compared to 9 in untreated soil sample of the same size, 27 Pseudosinella alba (Entomobryidae) versus 6, and 8 Orchesella villosa (Entomobryidae) versus none in respective samples.

Similar results were obtained from a previous field experimental method consisting of putting into a forest rendzine soil some 100 cc. desiccated soil samples of three grain sizes (1 - between 10 and 4 mm ; 2 - between 4 and 1 mm ; 3 - <1 mm) without fauna, and to check the rate of settlement on each sieved fraction at regular intervals (VANNIER, 1975). The return of soil animals from surrounding area was achieved for all zoological groups after 21 days. Collembola as Poduromorpha, and particularly Neelipleona and Entomobryomorpha reached a higher density in the coarse and middle fractions than ones in the natural undisturbed soil.

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QUESTIONS and COMMENTS

H. PETERSEN: Can your observation that oribatids are more important as immigrants into the acid treated soil cores than Collembola be explained by the low pH or by compounds evolved during heat treatments which are repellent towards Collembola? I noticed that the collembolan numbers in the alkaline soil cores culminated in the second week whereas oribatid numbers in acid soil cores culminated in the third week. Could the dominance of Collembola in the alkaline cores therefore be explained by their greater mobility, followed by competitive exclusion of the oribatids?

G. VANNIER: We need further precise information about selective recolonization upon heat desiccated soil samples. We can advance a lot of reasons to explain that certain animals are attracted and others excluded. In addition to your suggestions, I think that the enhancement of microflora growth is the most important factor of attraction. I mean, when a microarthropod invades a treated soil sample, it deposits some droppings from which a developm;ent of germs starts, precisely the germ strains it eats.

To answer your second question, I think mobility differences between mites and springtails are not too much involved in my experiment because the small size area of the treated soil samples. I collected samples each with an area of 20 cm^2.

H. KOEHLER: What role does the dispersal power play for the rehabilitation of the sterile soil?

Does the change in soil parameters (water content, texture, porosity) favor some specific colonizer groups?

G. VANNIER: Our experimental study did not last enough time (four weeks) to answer you about the role of dispersal power on the rehabilitation of the sterile soil. First we must look at the rehabilitation of germ balance which sways the microarthropods colonization. I'll keep in mind your interesting suggestion.

I don't think such parameters are involved because I am convinced that the colonization by microarthropods is mainly influenced by a fast microbial growth, enhanced by previous desiccation of soil samples.

THE ROLE OF INVERTEBRATES IN THE FUNGAL COLONIZATION OF LEAF LITTER

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INTRODUCTION

Various roles have been given to the arthropods which inhabit the forest litter community. While many of these roles are speculative due to difficulties in experimental methods and/or observations (Crossley, 1977), they have included fragmentation of the litter (Edwards and Heath, 1963) thereby enhancing surface area for microbial attack, substrate modification by fecal production (Nicholson et al., 1966; Webb, 1977), and dispersal of microbial spores either on the body surface (Jacot, 1930; Poole, 1959; Mignolet, 1971) or by passage through the gut in a viable state (Behan, 1978; Mignolet, 1971; Witkamp, 1960). In fact, many microarthropod species (mites, collembola) are known to actively feed on bacteria and fungi (the major decomposers in forest ecosystems), the latter being known to accumulate nutrients in their tissues to concentrations much greater than the surrounding habitat (Cromack et al, 1975; Stark, 1972). Thus the role of arthropods in nutrient cycling has been suggested (Crossley, 1976; Crossley and Witkamp, 1964). Therefore an important role of microarthropods is their catalytic interrelationship with microorganisms (Drift, van der, 1970; Ghilarov, 1963; Mignolet, 1972; Mitchell and Parkinson, 1976).

The purpose of this study was to investigate and quantify the role which litter arthropods play in the dispersal and fungal colonization of beech (Fagus grandifolia) leaf litter in a beech-maple climax community in extreme southwest Michigan at Warren Woods, Berrien County, Michigan, U.S.A.

METHODS AND MATERIALS

Two aspects of arthropod-microfungal interactions were studied. The first consisted of placing individuals of various arthropod orders singly onto agar media for a period of 24 to 48 hours at which time the individual was removed and saved for identification. In some cases fungal growth had covered the animal prior to removal so that identification was restricted to the level of order. All pertinent information concerning the date, and litter layer, the species identification as well as the fungal isolates obtained were recorded. A total of 459 litter organisms including 292 Acari, 49 Collembola, and 45 Diplopods were studied.

Originally an array of agar media was used for the invertebrates including potato dextrose agar, Czapek-Dox agar, and cellulose agar. Eventually soil extract agar was used exclusively as it was a non-selective media which isolated all the fungi. It also produced slower growth and increased sporulation due to its nutrient-poor composition. The resultant fungal colonies were subsequently isolated onto malt extract and/or Czapek-Dox agar slants for identification.

The second experiment involved the use of fine and medium nylon mesh litterbags of two sizes (5 and 500 microns respectively) which contained sterilized (via propylene oxide gas for a 72-hour period) and unsterilized beech leaf discs each in separate litterbags. Each litterbag (10 cm^2) contained 10-2.3 cm diameter leaf discs. These litterbags were placed into the forest leaf litter at the interface of the L-F horizons. After two weeks in the field the litterbags were aseptically returned to the laboratory whereby the leaf discs were plated individually either on soil extract agar or in damp chambers. The study consisted of two seasonal periods (Spring and Fall) corresponding to the previously determined population peaks of the microarthropods. Each season contained three sampling dates (May, June, and July) and (October, early December, and late December). For the spring season, ten sites were utilized within a date, each site containing four litterbags representing fine and medium mesh each with a sterile and unsterile set of discs. Thus a sampling date yielded 100 discs per litterbag treatment. Fifty of these discs were plated onto soil extract agar for isolation of fungi actively growing on the discs as well as any spores present. The remaining fifty were plated by damp chamber method whereby fungal growth was obtained from the leaf tissue only. The Fall season experimental design was similar with the following modifications. Only five sites were used per sampling date. Each site contained a set of litterbag treatments as in the Spring. In addition, a chlordane solution application was applied to a second set which was placed at the same sampling site. The chlordane treatment was devised as an additional method for excluding arthropods while not affecting the fungal populations (Brown, 1978).

All leaf discs were examined under a binocular microscope with fungal isolations, identifications and frequency of occurrences (presence or absence) recorded for each litterbag treatment. All data was compiled for computer analysis. Since the frequency of appearance of a particular fungi approximated the binominal distribution, an arcsine transformation of the percentages of leaf discs colonized per sampling unit produced homoscedasticity enabling analysis of variance to be performed.

RESULTS

Arthropods on agar plates

Four fungal genera commonly found on leaf litter (Penicillium, Cladosporium, Trichoderma, and Mortierella), were determined to be the most frequent isolates obtained from the litter invertebrates placed upon the agar media (Appendix A). A total of nine genera and twenty species were isolated (Pherson, 1979). The genus Penicillium was the most frequent isolate occurring on 56% of the individuals plated. This genus, however, contains over several hundred species of which more than twenty were identified from this study. The other three genera included single species of Cladosporium, Trichoderma, and Mortierella.

If this data is compared with the only similar study (Christen, 1975) a high diversity of fungal genera may be considered as potentially transported by these arthropod vectors although only the genera Penicillium, Cladosporium, and to a lesser extent Trichoderma and Mortierella were frequently carried. In addition, the number of genera isolated from an individual was, in many cases a function of size (Appendix B). Oligochaeta, Diplopoda, Coleoptera, and Araneida generally had a greater fungal generic diversity although much variation existed within an order (e.g. Acari, Collembola).

Litterbag experiments

The preliminary results of Pherson (1978) were confirmed with this investigation as the expanded litterbag experiments, utilizing a total of 2400 leaf discs, revealed reduced frequencies of colonization for three of the four arthropod-carried genera when the leaf discs were enclosed in the fine mesh. Analysis of variance (Appendix C) indicated that colonization frequency was both attributable to sampling DATE and TREATMENT effects. MEDIA influence, when present, showed the species favored soil extract agar. A more detailed analysis of variance of the treatment effects (mesh, sterilization) revealed that sterilization was usually significant. While this may be explained by the fact that the fungi colonizing these sterilized discs were unable to reach the frequencies of those discs not sterilized during the two week interval, it was not ascertained whether the propylene oxide had produced a time-lag for colonization. More importantly, there was also a significant mesh effect for Cladosporium, Trichoderma, and Penicillium, as follows: Cladosporium significantly colonized sterilized discs found within medium mesh more frequently than those within fine mesh during the Spring season. In the Fall, colonization was once again favored on medium mesh discs although statistical significance was lacking. Trichoderma was found to exhibit a similar pattern. Penicillium was determined to be significantly more frequent on sterilized discs in medium mesh litterbags than in fine mesh for both the Spring and Fall season. A significant chlordane effect was also observed for both Cladosporium and Trichoderma as it was found to reduce their presence.

DISCUSSION

It has been shown that a particular subset of the leaf litter microfungal community is carried disproportionately by leaf litter invertebrates. These fungi are considered by Swift (1976) to be resource non-specific or "generalists". They consist of four morphologically diverse fungal genera: a very abundant "dry-spored", air-borne primary colonizer (Cladosporium); an abundant "dry-spored", "soil fungus" (Penicillium); a wet-spored soil fungus (Trichoderma); and a soil fungus (which produces endogenous spores enclosed within a sporangium (Mortierella). All of these are known to be associated with deciduous leaf litter fungus succession (Hogg and Hudson, 1966; Hudson, 1968, 1971; Jensen, 1974; Saito, 1956).

It may be questioned why these particular fungi, among all those involved in the leaf litter decomposition process were carried by the leaf litter invertebrates. Among the possibilities include their prolific spore-producing capacity. *Cladosporium* is the most common air-borne fungi becoming so abundant that it is one of the major causes of "hay-fever" allergies. It is also one of the first surface colonizers of deciduous tree buds and leaves in the Spring. The other three fungi are generally categorized as "soil fungi". As such they are frequently noted as appearing on leaf litter from six months onward after leaf fall. However, *Penicillium* and *Trichoderma* are also known to be common indoor air-contaminants. The prolificity of all these fungi is reflected in their numerical abundance through soil dilution plate counts (Jensen, 1963).

Another possibility is that there exists specialized dispersal mechanisms and/or adaptive morphological features. A close examination of the conidia (exogenous spores) of *Cladosporium*, *Penicillium*, and *Trichoderma* and the sporangiospores (endogenous spores) of *Mortierella* reveal highly disparate morphologies. *Cladosporium* conidia are large and barrel-shaped; *Penicillium* conidia are minute and round to elliptical, *Trichoderma* conidia are similar in size to *Penicillium* but are wet due to a mucilaginous substance; while *Mortierella* spores are small and enclosed within a saclike sporangium which "dissolves" upon contact with another surface.

Even the enzymatic capacities of these fungi are variable. It is generally state that the primary colonizers (e.g. *Cladosporium*) can produce a wide array of enzymes (Pugh, 1974), first attacking the easily decomposable sugars on the leaf surface and later when the leaf becomes senescent, penetrating the cuticle and attacking the cell walls. Meanwhile the most persistent fungal flora, those found in the soil, generally have this potential as well as for antibiotic production (*Penicillium* and *Trichoderma*). Indeed *Penicillium*, *Cladosporium*, and *Trichoderma* are able to decompose cellulose. Interestingly *Penicillium*, *Trichoderma*, and *Mortierella* are capable of decomposing chitin (Hudson, 1972). This prompts speculation that invertebrates carry fungi which may actually attack their own integument. Studies of insect fungal parasites (Madelin, 1968) however show that only *Penicillium* may be parasitic even though it probably occurs through integumental wounds. Nevertheless, my studies have demonstrated that those individuals which died while on agar media yielded *Penicillium* and *Mortierella* growing from their bodies. Alternatively, this chitin-decomposing capacity may enable these species to attack the cell walls of other fungi.

Litterbag experiments have been used previously to demonstrate the role of invertebrates in leaf litter breakdown (Edwards and Heath, 1963) and for assessment of microarthropod populations (Crossley and Hoglund, 1962). This investigation used litterbags to determine whether invertebrate-carried fungi would be reduced in colonization frequency on leaf material if the invertebrates were prevented from entering. The results tend to support this premise for three of these fungi (*Penicillium*, *Cladosporium*, *Trichoderma*).

Several alternative explanations, however, do exist which must first be examined. These include spore size, hyphal growth activity, litterbag micro-environments, and water dispersal. These are explained as follows: *spore size* - only *Cladosporium* can be excluded from entering the fine mesh due to its large spores. Both *Trichoderma* and *Penicillium* are small enough to enter and have done so in laboratory experiments; *hyphal growth activity* - if differential growth rates occur for a particular genera, colonization may be affected.

This seemed unlikely as all fungi possessed rapid growth rates for colonization over a two-week period. (D. Wicklow, pers. comm.). Also hyphae/mycelia were small enough to easily pass through the fine mesh; litterbag microenvironments - while evidence is available to suggest a modification influence (Anderson, 1973), if strongly present, this would have been demonstrated in major frequency differences between mesh sizes containing unsterilized discs. This effect was infrequently observed; water dispersal - while water may be important in fungus dispersal (Bandoni and Koske, 1974), especially for wet-spored species, this was not observed for Trichoderma, even though it could pass into the fine mesh bags.

Circumstantial evidence therefore suggests that frequency reduction in fine mesh litterbags may be due to the inability of microarthropods to enter. If true, in what ways may microarthropods influence the colonization of leaf litter microfungi, its successional pattern, and its ultimate effect on decomposition and nutrient release? While most studies show that microarthropod species (mites, collembola) are primarily generalist feeders (Anderson, 1975; Anderson and Healey, 1972; Luxton, 1972), feeding preference studies (Christen, 1975; Hartenstein, 1962; Luxton, 1972; Mitchell and Parkinson, 1976) have shown that Cladosporium and Trichoderma are among the most preferred. This provides speculation that a possible mutualistic interaction analogous to pollination and seed dispersal systems may be operating whereby the animal while feeding upon a colony becomes encrusted with additional spores which are then carried about. Additionally, some of the spores or hyphae may pass through the gut in a viable state (Behan, 1978; Christen, 1975; Mignolet, 1971; Poole, 1959; Witkamp, 1960). This mutualistic effect may provide additional stability (May, 1973) to the leaf litter community structure.

Fungal successional patterns may be indirectly influenced by this arthropod dispersal. Swift (1976) states that one of the potential actions of primary fungal colonizers may be to metabolize modifier compounds (polyphenols, tannins) in leaf litter thereby increasing its palatability to soil animals. These animals, in turn may be of potential significance in the spore dispersal of the later colonizers. The results from this study provides supportive evidence.

Finally, it is suggested that man-made disturbances upon leaf litter arthropod populations (e.g. pesticides) may potentially alter the leaf litter community structure, not only by reduction in litter fragmentation but by modifying fungal succession through loss of dispersal vectors.

CONCLUSIONS

It is apparent that a particular generic subset (Penicillium, Cladosporium, Trichoderma, and Mortierella) of the leaf litter microfungal community is carried by various arthropod orders in beech (Fagus grandifolia) leaf litter. Of those arthropod-carried fungi, three (Penicillium, Cladosporium, Trichoderma) exhibit significantly reduced colonization frequencies when sterilized leaf discs are enclosed in fine (five micron) nylon mesh litterbags which exclude the microarthropods. While various alternative hypotheses are shown to be only partially plausible, circumstantial evidence does suggest an arthropod-dispersal phenomenon.

It is speculated that potential effects of man-made disturbances (e.g. pesticides) on forest leaf litter may affect microarthropod populations which in turn may alter fungal colonization, decomposition and nutrient cycling processes.

ACKNOWLEDGEMENTS

I wish to thank the Department of Natural Resources, the State of Michigan for permission to work in Warren Woods State Park. I also wish to thank my wife, Janette, for her assistance in the preparation of this manuscript.

APPENDIX A. Number and frequency (in parentheses) of selected fungal genera isolated from a variety of live litter organisms from Warren Woods, Michigan, U.S.A.

Order	N	Penicillium	Cladosporium	Trichoderma	Mortierella
Acari	292	149 (.51)	31 (.10)	14 (.05)	20 (.07)
Collembola	49	37 (.76)	4 (.08)	8 (.16)	1 (.02)
Psocoptera	6	3 (.50)	1 (.14)	-	-
Pseudoscorpionida	4	4 (1.0)	1 (.25)	-	-
Diplopoda	45	20 (.44)	2 (.04)	5 (.11)	6 (.13)
Chilopoda	4	4 (1.0)	-	-	-
Isopoda	5	5 (1.0)	-	-	-
Coleoptera (Staphylinidae, Carabidae)	14	11 (.78)	-	-	3 (.21)
Diptera larvae (Unidentified)	4	2 (.50)	1 (.25)	-	2 (.50)
Araneida (Linyphidae)	25	15 (.50)	10 (.33)	3 (.10)	-
Oligochaeta	11	6 (.55)	2 (.18)	5 (.45)	1 (.09)
TOTALS	459	256	52	35	33
FREQUENCY	-	.56	.11	.08	.07

APPENDIX B. Fungal genera diversity associated with beech leaf-litter invertebrates

Species	N	$\bar{X}$ no. fungal (genera) per animal
Acari:		
Galumma ithacensis	76	.46 ± .74
Phthicaracarus setosum	51	.25 ± .48
Hypochthonius rufulus	8	.25 ± .46
Scheloribates sp.	17	.53 ± .80
Unidentified (Oribatid)	38	1.10 ± .34
Veigaia nemorensis	9	.67 ± .50
Collembola:		
Entomobryoides purpurascens	4	1.25 ± .96
Isotoma albella	14	2.21 ± 1.37
Frisea claviseta	14	.50 ± .65
Ptenothrix marmorata	6	1.17 ± .55
Diplopoda:		
Unidentified sp.	31	1.29 ± 1.07
Araneida:		
Linyphiidae	10	1.30 ± .82
Oligochaeta:		
Lumbricidae	9	2.0 ± 1.41
Coleoptera:		
Staphylinidae	7	1.43 ± .98

APPENDIX C. ANALYSIS OF VARIANCE FOR LITTERBAG EXPERIMENTS

	ALTERNARIA	CLADOSPORIUM	EPICOCCUM	TRICHODERMA	MUCORALES	PENICILLIUM
SPRING						
Date	***	***	***	**		***
Treatment	**	***	***	***		***
Media		*	***	***	***	
Interaction	***	***	***	***	*	***
Treatment:						
Mesh		**		***		***
Sterilization	**	***	**	***		***
Interaction		**	**			***
FALL						
Date	***	***	***	***	***	**
Treatment	***	***	***	***	*	*
Media	***		**	***	***	**
Interaction	***	***	***	***	***	*
Treatment:						
Mesh						**
Sterilization	***	***		***		
Chlordane		***		**	*	
Interaction	**	**	**			

Significance Level .05 = * .01 = ** .001 = ***

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QUESTIONS and COMMENTS

S.B. HILL: I was interested in your comment regarding chitin decomposition by fungi. I once worked with an insectivorous bat guano medium,which consisted largely of chitin. It supported one species of fungus, *Penicillium janthinellum* and one species of oribatid mite, *Rostrozetes foveolathus* comprised 80% of the mesoarthropod population and it appeared to be feeding primarily on the *Penicillium.* I had previously concluded that the low pH (4.00) and the antibiotic activity of the *Penicillium* was responsible for the absence or low population density of other species of microarthropods. Now I wonder if they may have been directly attacked by this *Penicillium*. I would be interested in your comments on this.

D.A. PHERSON: I feel that your conclusions are justified. Little is known of the enzymatic capacities of individual species of the genus *Penicillium* to confidently state that cuticular attack is responsible for the absence of other microarthropod species. Rather it appears that *Rostrozetes foveolatus* is particularly adapted to feeding on that *Penicillium* species without suffering from any antibiotic effects.

EVOLUTIONARY ASPECTS OF MYCOPHAGY IN *Ariolimax columbianus* AND OTHER SLUGS

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INTRODUCTION

Large size, mobility, and terrestrial habits frequently preclude slugs from biological investigations of decomposition, nutrient cycling, and other aspects of soil zoology. Only through recent studies of consumption, assimilation, and excrement production (Pallant, 1969, 1970, 1974; Newell, 1967, 1971; Jensen, 1975; Jennings and Barkham, 1976; Richter, 1979) has slug importance in biomass, energy, and nutrient transfers within soils been clarified. Clearly, these studies show that slug consumption of fresh, sensescent, and dead vegetation directly influences plant decomposition and soil humification.

An indirect and perhaps more significant way by which slugs influence decomposition and other aspects of community ecology may result from slug feeding on fungi (mycophagy) and the concomitant dispersal of spores. Fungi are primary agents of decomposition, serious saprophytes, and form essential mycorrhizal associates with plants; thus their dispersal by slugs may significantly influence more involved aspects of community dynamics.

Slugs feed on a variety of plant and animal matter (Runham and Hunter, 1970), including fungi in the coniferous forest of western Washington, where both slugs (specifically, Ariolimax columbianus Gould) and fungi are especially numerous. There are no published accounts of mycophagy in Ariolimax and only few literature accounts of slug feeding on fungi in North America (Buller, 1909, 1922; Gregg, 1944; Ingram, 1949; Hand and Ingram, 1950). Accounts of slug mycophagy in Europe are more numerous and indicate that most slugs are mycophagous and eat a wide variety of fungi. Generally, authors itemize fungi ingested by slugs (Taylor, 1907; Benecke, 1918; Elliott, 1922; Kittel, 1956), although in Frömming's (1940, 1954, 1962) publications consumption was quantified.

The purpose of the present study is to document mycophagy in Ariolimax and analyze its relationship to fungal taxonomy, distribution, phenology, and nutritional value. Results will be interpreted within an evolutionary context in which fungal density, availability of alternate foods, caloric and chemical composition, and other factors important in determining herbivore diets (Schoener, 1971; Pulliam, 1974, 1975) will be investigated. Potential reproductive benefits accruing to fungi from slug mycophagy will also be considered.

SPECIES DESCRIPTION AND STUDY AREA

Ariolimax columbianus is the dominant and largest indigenous slug throughout the wet coniferous forests of western North America, often attaining a length of 15 cm and a weight of 20 grams. Seasonal activity extends from April through October when temperatures are between 7°C and 25°C (Richter, 1976). Maximum densities of slugs within the study area were estimated at 2500 per hectare, with a total consumption of 62 kg/ha/yr (Richter, 1979).

Field observations were conducted in a second growth Pseudotsuga menziesii (Tsuga heterophylla zone, Franklin and Dyrness, 1973) forest located 55 km east of Seattle, Washington. The dominant trees include P. menziesii, Alnus rubra, Acer circinatum, and Prunus emarginata. Common shrub and herb species are Pteridium aquilinum, Gaultheria shallon, Berberis nervosa, Polystichum munitum, and Linnaea borealis. Abundant epigeous fungi include members of the families Russulaceae (e.g., Russula emetica and Lactarius aurantiacus), Boletaceae (e.g., Suillus lakei and Boletus zelleri), Tricholomataceae (e.g., Laccaria amethystina and L. laccata), and Cantharellaceae (e.g., Cantharellus cibarius).

METHODS

Slug feeding was observed along transects surveyed at least twice weekly during the study period. Noted during each feeding observation were length of feeding bout, host age, host part eaten, and the relative density of host and its surrounding vegetation. Feeding preference for eaten fungi and plants was calculated using Ivlev's (1961) selectivity coefficient (E) in which preference is calculated as the relation between the food item in the diet and the habitat according to

$$E = \frac{r_i - p_i}{r_i + p_i}$$

where

r_i = percentage of item in the diet

p_i = percentage of item in the habitat

Inorganic nutrient analysis for lichens and senescent leaves, unless otherwise referenced, follows the methods outlined by Piper (1944) and Jackson (1958).

Separate laboratory experiments were conducted to clarify different aspects of mycophagy. In the first group of experiments, a slug starved for 24 hours and one mature sporocarp were placed in several different 1-liter plastic cups. For 30 minutes slugs were continually observed through clear lids under subdued light. Observations were recorded for this 30-minute period and again 24 hours later to assess diel feeding.

To determine selectivity, an array of 17 species of fungi were distributed in a circle within a 50- x 50- x 200-cm wooden box whose base was covered with 2 cm of moist soil. Within the sporocarp ring, five slugs were placed so that each animal faced in a different direction. Each slug was subsequently observed and the data recorded on fungi and part eaten, as described in the cup experiment.

Phenological preferences were specifically tested in a set of experiments in which starved slugs were offered immature and mature sporocarps of several species. One starved slug was placed in each container with either a young or mature sporocarp. After 24 hours observations were again made on fungi and part eaten.

RESULTS

Feeding Behavior

In the field, *Ariolimax* was frequently observed to orient, crawl towards, and feed extensively on epigeous fungi. They crawled directly towards *Russula emetica* and *Laccaria laccata* which had been picked and placed up to 2 m away. In laboratory feeding trials, slugs were observed to immediately orient and move towards edible species 0.5 m away. Observations and documentation that slugs exhibit a highly developed sense of smell (Kittel, 1956; Runham and Hunter, 1970) and that many mature fungi give off strong odors (Maser, Trappe, and Nussbaum, 1978; Miller, 1978), support my observations that *Ariolimax* locates edible species by olfaction.

Importance of Mycophagy

Mycophagy accounted for 11% and 5% of 1973 and 1974 feeding observations (Richter, 1976) and was limited to a few epigeous basidiomycetes such as *R. emetica*, *R. pologonia*, *R. placata*, *Lactarius obnybylus*, and *Boletus zelleri*. Common but uneaten fungi included *Amanita silvicola*, *Coltricia perenis*, *Cantharellus cibarius*, *Lyophyllum multiceps*, and the ascomycete *Helvella lacunosa*. Feeding on *R. emetica* accounted for more than 50% of total feeding observations, with the balance being distributed among other Russulaceae, Tricholomataceae, and Boletaceae. Mycophagy, as expected, primarily occurred in October when sporocarps were abundant. During this month, fungi accounted for 39% and 13% of the 1973 and 1974 diets, respectively. Lower dietary importance of fungi in 1974 reflects temperatures above and precipitation below the 10-year norm, which reduced sporocarp production and extended availability of vegetation.

The Shannon-Weaver diversity index was applied to observed slug diets. H' was calculated from the equation

$$- \sum_{i=1}^{S} pi \log pi$$

and corrected for the bias of the estimate (Poole, 1974), and indicated that slug feeding is responsive to sporocarp production and vegetation phenology. A 0.98 October 1973 value quantifies and supports the observation that slugs feed on few food sources, of which fungi were the major component. A significantly higher 1974 value of 1.54 suggests that diet was more diverse than in 1973 and indicated that sporocarps and plants exhibited equal numerical importance.

Field Preferences for Fungi and Hymenium

Inspection of Table 1 shows that, of six categories of food items eaten, fungi and the lichen *Parmelia* were the most preferred (index +0.9). However, feeding bouts on fungi was significantly longer than on *Parmelia* sp. and alternative items (Extended Median Test, $P < 0.5$; Conover, 1971). Mean feeding bouts on sporocarps averaged 47 and 48 minutes during 1973 and 1974, whereas on *Pteridium aquilinum*, the second most popular item, feeding was significantly lower, at 27 and 32 minutes, respectively ($P < 0.01$). Although *P. aquilinum*, senescent leaves, and other foods were eaten more frequently than fungi in 1974, and *Parmelia* sp. exhibited an identical preference index as fungi in both years, only slugs feeding on fungi exhibited higher composite values of frequency, preference, and length of feeding bouts.

TABLE 1. Importance of and preference for fungi, lichen, and other items in the October diet of *Ariolimax* (---- = value undetermined)

Dietary Component	Number of Observations 1973	Number of Observations 1974	% of Total Observations 1973	% of Total Observations 1974	Preference Index 1973	Preference Index 1974	Feeding Time (minutes) 1973	Feeding Time (minutes) 1974
Fungi (e.g., *Russula emetica*)	14	10	39	13	+0.9	+0.9	47	48
Lichen (e.g., *Parmelia* sp.)	4	12	11	16	+0.9	+0.9	36	14
Senescent deciduous leaves (e.g., *Alnus rubra*)	5	16	14	21	+0.6	0.0	28	36
Senescent forest herbs (i.e., *Pteridium aquilinum*)	12	23	33	30	+0.4	+0.4	27	32
Others (e.g., *Trillium ovatum*)	----	8	----	11	----	+0.8	----	12
Fruit (i.e., *Gaultheria shallon*)	1	7	3	9	−0.8	−0.4	15	19

In addition to *Ariolimax*'s preference for fungi over other foods, slugs preferred certain fungal parts over others. Combined two-year feeding data reveal that, of 24 feeding observations, 83% were restricted to mature sporocarps and of these 85% to the hymenium. The stipe was preferred in all four immature specimens eaten and only accounted for 15% of feeding on mature fungi, while the pileus was not observed to be eaten during any feeding bout. Clearly, the hymenium is preferred over the stipe or pileus in mature fungi and the stipe over other parts in immature sporocarps (Chi square = 11.2, $P < 0.01$, df = 2).

Laboratory Preferences

Many fungi, including *A. silvicola*, *C. cibarius*, and *H. lacunosa*, which were common but not observed to be eaten in the field, were eaten during laboratory preference tests. This may be expected as the short 48-minute field feeding bout increases the possibility that less preferred fungi may have gone unrecorded. Additionally, starved laboratory slugs, when offered limited choice, are more inclined to feed on low preference species. Only three species, *Coprinus atramentarious*, *Lactarius aurantiacus*, and one unidentified Cortinariaceae, were avoided both in field and laboratory. In total, 18 of 21 (86%) tested species were eaten without any immediately apparent ill effects. These data suggest that many more fungi may contribute to autumnal food requirements than are suggested from field observations alone.

Taxonomic trends in slug feeding preferences are apparent for those families represented by the several species of fungi eaten during testing (Tables 2 and 3). Generally palatable to *Ariolimax* are the Boletaceae (represented by one genus, three species), Russulaceae (represented by two genera, five species), and Tricholomataceae (represented by five genera, six species). *C. atramentarious* (Coprinaceae), *Cortinarius* sp. (Cortinariaceae), and *L. aurantiacus* (Russulaceae) were not eaten. *Russula* sp. and *Lactarius sanguifluus* were the two species most readily eaten, followed by *R. emetica*, *L. multiceps*, and *Boletus* sp. Although *R. emetica* is not always the most preferred as determined by laboratory tests, it remains the most important to *Ariolimax* because of its density and ubiquitous distribution.

In the cup experiment, in which *Ariolimax* was given no alternative to the test species, 13 of 17 (76%) fungi were eaten (Table 2). Only five (29%) species were fed upon during the first 30 minutes of testing; the remaining species were eaten within 24 hours. Results of the smorgasbord test, in which slugs chose from among 17 simultaneously available species, were similar to the cup test. However, two species, *L. laccata* and *Collybia* sp., were not eaten, and one species, *Boletus mirabilis*, was eaten in the smorgasbord but not in the cup test (Table 3). Feeding on nine (53%) species, five of which were also promptly eaten in the cup experiment, commenced within the first half hour. However, since five slugs were tested in each replication of the smorgasbord test, a greater probability of observing some prompt feeding would be expected.

TABLE 2. Results of cup palatability tests on 17 species of fungi including replications, start of feeding, minutes of feeding, and fungal part ingested (U = undetermined, N = no feeding observed, H = hymenium, P = pileus, S = stipe, 1 = feeding initiated within 15 minutes, 2 = feeding initiated between 15 and 30 minutes, 3 = feeding initiated after 30 minutes)

Fungi	Σ Replications	Number of Replications In Which Species Eaten	Feeding Interval	Feeding Time In Minutes	Sporocarp Part Ingested
Ascomycetes					
Helvellaceae					
Helvella lacunosa	1	1	2	30	S
Basidiomycetes					
Amanitaceae					
Amanita silvicola	2	1	1	40	H
Boletaceae					
Boletus mirabilis	1	0	N	N	N
Boletus zelleri	1	1	3	U	H
Suillus lakei	2	2	1, 1	45, 40	H
Cantharellaceae					
Cantharellus cibarius	2	2	1, 2	25, 30	P, H
Coprinaceae					
Coprinus atramentarious	1	0	N	N	N
Cortinariacea					
Cortinarius sp.	1	0	N	N	N
Russulaceae					
Lactarius aurantiacus	1	0	N	N	N
Lactarius sanguifluus	2	2	3, 3	U, U	H, H
Russula cascadensis	1	1	3	U	H
Russula emetica	2	2	1, 3	45, U	H, H
Russula sp.	2	2	3, 3	U, U	H, H
Tricholomataceae					
Collybia sp.	1	1	3	U	H
Laccaria amethystina	2	2	2, 3	35, U	H
Laccaria laccata	2	1	3, N	U, N	H
Lyophyllum multiceps	1	1	3	U	H, S

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TABLE 3. Results of smorgasbord palatability tests on 17 species of fungi including replications, start of feeding, minutes of feeding, and fungal part ingested (U = undetermined, N = no feeding observed, H = hymenium, P = pileus, S = stipe, 1 = feeding initiated within 15 minutes, 2 = feeding initiated between 15 and 30 minutes, 3 = feeding initiated after 30 minutes)

Fungi	Σ Replications	Number of Replications In Which Species Eaten	Feeding Interval	Feeding Time In Minutes	Sporocarp Part Ingested
Ascomycetes					
Helvellaceae					
Helvella lacunosa	2	1	3	40	S
Basidiomycetes					
Amanitaceae					
Amanita silvicola	5	3	1, 1, 3	15, 30, U	H, HS, H
Boletaceae					
Boletus mirabilis	3	2	3, 1	U, 10	H, H
Boletus zelleri	2	2	3, 2	U, 30	H, H
Suillus lakei	2	2	3, 2	U, 25	H, H
Cantharellaceae					
Cantharellus cibarius	5	2	1, 1	15, 15	H, H
Coprinaceae					
Coprinus atramentarious	3	0	N	N	N
Cortinariacea					
Cortinarius sp.	3	0	N	N	N
Russulaceae					
Lactarius aurantiacus	2	0	N	N	N
Lactarius sanguifluus	5	3	3, 3, 1	U, U, 40	H, H, H
Russula cascadensis	3	1	2	25	H
Russula emetica	5	3	2, 3, 3	30, U, U	HP, H, H
Russula sp.	5	5	3, 3, 3, 3, 3	U,U,U,U,U	H,H,H,H,H
Tricholomataceae					
Collybia sp.	3	0	N	N	N
Laccaria amethystina	5	2	2, 1	25, 15	H, H
Laccaria laccata	5	0	N	N	N
Lyophyllum multiceps	2	2	3, 2	U, 20	H, S

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Although the same fungi were generally eaten in both experiments, feeding bouts for single slugs in cups were longer on five of six eaten species. This difference may be accounted for by the fact that slugs had only one type of fungi from which to choose and no secondary stimuli from other fungi species. The pileus and stipe are occasionally eaten; however, 90% of mycophagy occurred on gills in both the cup and smorgasbord experiments (Tables 2 and 3), thus indicating a preference for the hymenium and confirming field observations.

Table 4, depicting the laboratory results of Ariolimax's feeding on young and mature fungi, indicates that, of the four species eaten, a preference was exhibited for mature sporocarps (Chi square = 17.71, $P < 0.001$, df = 1). In two of the four species, Mycena haematopus and Naematoloma fasciculare mature sporocarps were almost exclusively eaten. In the other two species, R. emetica and Amanita muscaria, both young and mature specimens were eaten; however, a greater proportion of mature, rather than immature, sporocarps were consumed.

TABLE 4. Results of *Ariolimax* feeding on young and mature fungi (A = species avoided regardless of age, P = probable difference attributable to age)

Fungi	Young Sporocarps Eaten			Mature Sporocarps Eaten			General Result
	Yes	No	Σ	Yes	No	Σ	
Ascomycetes							
Hellvellaceae							
Helvella lacunosa	0	5	5	0	5	5	A
Basidiomycetes							
Amanitaceae							
Amanita muscaria	4	3	7	5	1	6	P
Cantharellaceae							
Cantharellus cibarius	0	5	5	0	5	5	A
Russulaceae							
Russula emetica	3	7	10	10	0	10	P
Strophariaceae							
Naematoloma fasciculare	1	6	7	4	3	7	P
Tricholomataceae							
Marasmius oreades	0	3	3	0	5	5	A
Mycena haemotopus	0	4	4	6	1	7	P

DISCUSSION

Ariolimax columbianus, like other slugs, feeds heavily on fungi. Taylor (1907) indicated that *Arion subfuscus* Drap. (*fuscus* Mull.) showed a preference for fungi and Elliott (1922) found that *Limax maximus*, *L. cinereoniger* Wolf (*maximus* L.), and *Arion ater* L. fed on most of 60 species of fungi tested, although *Arion circumscriptus* Johnst, *Limax arborum* Bouch (*marginatus* Mull.), and *Milax sowerbyi* Fer. showed low feeding preference for many of the same species. In extensive studies Fromming (1954) determined that both *Arion intermedius* Norm. and *Limax tenellus* Nilss. ate all of 24 tested species, although *A. intermedius* never ate the quantities observed eaten by *L. tenellus*.

Certain factors may explain the widespread use of fungi by slugs. According to optimum foraging theory, slugs should respond to changing food density and quality by selecting those items that maximize growth and reproduction (Schoener, 1971). Additionally, theory postulates that nutritious food sources should favor specialization, whereas poorer sources should lead to generalization with respect to diet (Morse, 1971; Schoener, 1971). Recent refinements to herbivore feeding theory have also encompassed aspects of plant phenology (Feeny, 1970; McKey, 1974) and coevolutionary strategies between hosts and animals in that plant defensive chemistry determines the breadth of herbivore diets (Rhoades and Cates, 1976; Rhoades, in press).

Food Density

During October, when epigeous Basidiomycetes are most abundant (Littke, 1978), *Ariolimax* preferentially feeds on fungi to the exclusion of other available and commonly eaten foods. Fungi availability certainly accounts for their numerical importance in the diet; however, abundance alone cannot account for the extensive mycophagy observed in *Ariolimax* and other slugs. Nutritional characteristics, including physical and chemical defenses and caloric and elemental composition, are also expected to be important. In autumn nutrition is especially significant to *Ariolimax* and other long-lived slugs which must store reserves prior to winter brumation.

Food Quality

Physical Defenses. Fungi may possess morphological specializations that are effective against slugs. Field and laboratory observations on *Ariolimax* and other slugs (Frömming, 1954, 1962) indicate that both the pileus and stipe may be better protected from grazers than the spore-bearing hymenium. For example, hyphae of the highly preferred hymenium are sparse and thin-walled when compared to the less preferred stipe and pileus, in which hyphae are densely intertwined and comparatively thick-walled (Pilát and Ǔsák, 1958). Additionally, chitin is the major cell wall material of both Ascomycetes and Basidiomycetes and is found in significantly higher concentrations in the stipe than pileus (Frömming, 1962). Although slugs have the capacity for hydrolyzing chitin (Runham and Hunter, 1970), the energy required for extracting nutrients may be prohibitive.

Hyphae may further be categorized as forming shaggy fibrils or scales on the pileus and stipe and spines or teeth on the hymenium, as observed in Hydnaceae. These characteristics could additionally function as physical deterrents to invertebrate mycophagists. Because species with these unique adapatations were not represented among those fungi tested, it is unknown to what extent these specializations influence palatability or the role structural characteristics play in defense, reproduction, and other functions.

Chemical Defenses. Buller (1909) suggested that toxins protect fungi from slugs. This contention is directly supported by my unpublished observations, in which several *L. maximus* died from feeding on immature *Amanita muscaria*, and those of Taylor (1907) and Elliott (1922), in which slugs succumbed after devouring other species. Considering all the chemicals isolated from fungi (Cochrane, 1958; Shibata, Natori, and Udagawa, 1964), one may certainly expect to find species toxic to slugs. Alkaloids which are known to deter herbivory and result in poor growth and reproduction in several invertebrates (Levin, 1976*a*, 1976*b*) are prevalent in fungi (Tyler and Stuntz, 1962, 1963) and could similarly affect slugs. Differential susceptibility of slug species and individuals within a species to fungi may also be expected (Crawford-Sidebotham, 1971).

Nutritional Aspects. Fungi rank high in both caloric and chemical content when contrasted to alternative dietary components. Caloric values of 4.1 to 5.2 kcal gm^{-1} dry weight in fungi are higher than values found in senescent forest herbs, and comparable to values calculated for senescing leaves of deciduous trees (Table 5). Since fruits generally have higher caloric values, fruits of *Gaultheria shallon* probably would exhibit caloric values between 5 and 6, similar to that of *Vaccinium deliciosum*.

During autumn chemical content of many plants is at its lowest (Lugg and Weller, 1948; Fraenkel, 1953) because leaf senescence is accompanied by a sharp reduction in N (Edel'man, 1963; Richter, 1979) and frequently other nutrients including P, K, Ca, Mg, etc. (Richter, 1979). Fungi therefore become increasingly valuable to slugs for their high concentrations of these elements (Cochrane, 1958) and for the organic compounds they contain (Singer, 1961). For example, fungi exhibit significantly higher percentages of protein than senescent leaves of *Pteridium aquilinum*, *Trillium* sp. *Dicentra* sp., and the lichen *Parmelia*. Similarly, carbohydrate content in fungi is substantially higher than in available *P. aquilinum* and probably also higher than that found in *Parmelia* and the senescent leaves of both herbs and trees (Table 6). Some fungi are considered excellent sources of nicotinic acid, riboflavin, niacin, and pantothenic acid, and a fair source of vitamins B, C, E, and K (Singer, 1961), which may additionally be valuable in supplying slugs with certain trace compounds unavailable from other sources.

That slugs particularly relish the hymenium is demonstrated in this and numerous other studies (Buller, 1909; Benecke, 1918; Frömming, 1954, 1962). It is interesting to note that the hymenium exhibits a 13% to 20% higher caloric value than the pileus or stipe (Smith, 1965), and

TABLE 5. Caloric composition of fungi, senescent vegetation, and fruit, of which the same or similar species are eaten by *Ariolimax* and other slugs

Dietary Component	Kilocalories/Gram^{-1} Dry Weight	Reference
Fungi		
Russula decolorans		
Hymenium	4.8	Smith, 1965
Pileus	4.0	Smith, 1965
Stipe	4.2	Smith, 1965
Suillus tomentosus		
Hymenium	5.2	Smith, 1965
Pileus	4.2	Smith, 1965
Stipe	4.1	Smith, 1965
Senescent Forest Herbs		
Trillium recurvatum	3.9	Kieckhefer, 1962
Dicentra canadensis	4.0	Kieckhefer, 1962
Senescent Deciduous Leaves		
Alnus rubra	4.6 – 5.8	Jensen, V., 1974
Acer rubrum	4.4	Jensen, V., 1974
Fruit		
Vaccinium deliciosum	5.3	Smith, 1970

TABLE 6. Chemical composition of fungi, lichen, and senescent vegetation, of which the same or similar species are eaten by *Ariolimax* and other slugs (---- = value undetermined, *protein = N x 6.25)

Dietary Component	Percent Dry Weight Protein	 Fat	 Carbohydrate	 Ash	Reference
Fungi					
Boletus edulis	32–35	5	58-59	6–8	Singer, 1961
Lactarius deliciosus	27	7	28	6	Singer, 1961
Tricholorma favovirens	15–18	----	71-78	7–11	Singer, 1961
Agaricus sp.					
Pileus	62	3	----	7	Singer, 1961
Stipe	48	1	----	7	Singer, 1961
Lichen					
Parmelia sp.	5*	----	----	----	Richter, 1979
Senescent Forest Herbs					
Pteridium aquilinium	9[1]	2[2]	14[3]	5[3]	1) Moon and Pal, 1942 2) Shearer, 1945 3) Williams and Foley, 1976
Trillium recurvatum	12	----	----	----	Kieckhefer, 1962
Dicentra canadensis	9	----	----	----	Kieckhefer, 1962
Senescent Deciduous Leaves					
Alnus rugosa	11[1]	----	----	8–14[2]	1) Kaushik and Hynes (1971) in Willoughby, 1974 (angiosperm litter) 2) Jensen, V., 1974

that the hymenium, including the pileus, has a 33% higher protein content than the stipe (Singer, 1961). Because the value of food lies in its digestability as well as its nutritional content, it is significant to note that, of six leaves of plants and the fungi Armillaria [Armillariella] mellea fed to A. ater, both highest consumption and assimilation rate occurred when this slug ate Armillariella (Jennings and Barkham, 1976).

Mycophagy and Reproductive Success of Fungi

As early as 1889, Stahl observed massive quantities of germinating spores of Morchella esculenta in the feces of Arion empiricorum. However, Voglino (1895) first suggested that slugs are important agents of spore germination and dissemination in epigeous fungi. Specifically, Voglino observed improved germination in spores of numerous species of fungi which had first passed through a slug's digestive tract. For some species, he observed that spores required slug digestive fluid as a prerequisite to germination.

Buller (1909, 1922) disclaimed a symbiotic relation between slugs and fungi, contending that slugs are troublesome ectoparasites affording no advantage to fungi. However, Buller must now be reevaluated in context of current fungi ecology. For example, it has long been known that fungi must depend on readily available organic substances for growth and reproduction, but it has only recently become established that the essential ectomycorrhizal associations that many fungi must form in order to take up required nutrients occur within a few select hosts (Trappe, 1962). In addition, information based on induced germination in spores of ectomycorrhizal fungi within slug digestive enzymes (Bowen and Theodorous, 1974, in Fogel and Trappe, 1978) suggests that slugs may be significant in ensuring the success of these essential associations.

Furthermore, the dispersal of fungi among their mycorrhizal associates may be aided by slug feeding behavior. Ariolimax, for example, exhibits host fidelity (i.e., feeds on relatively few core species), thus facilitating the dispersal of spores between different individuals of the same species. Slugs thus offer a directional component to spore dispersal that would be unattainable from wind or water dissemination. Although most spores are likely to be excreted within a few days following feeding, Hasan and Vago (1966) found that spores in slugs were regularly excreted and viable within feces for eight days, a sufficient time for slugs to find conspecifics of the original fungal host or other suitable mycorrhizal associates, depending on fungi specificity.

Slug feces possess the necessary biological and physical traits of a good germinating substrate. Slug feces provide nutrition for developing mycelia (Wagner, 1896; Neger, 1908; Hasan and Vago, 1966). Both chlamydospores and hyphae exhibit narrow tolerances of humidity, temperature, and pH (Lamb and Richards, 1974), which to some extent is favorable in slug feculae. Thus slug feces provide a readily available and favorable innoculum which is important for oidia and basidiospore germination and has been shown to be essential to chlamydospore and hyphae survival.

Slug preferences for the hymenium of certain fungi, the mixing within crop and intestine of spores and hyphae from conspecifics, host fidelity, and the nonrandom distribution of innoculated feces greatly facilitate recombination and outbreeding. These actions are especially important to "the great majority of higher fungi... characterized by obligatory crossmating, and, in all cases, self-sterility is imposed by an incompatibility mechanism" (Raper, 1966, p. 39). Slug feeding and dispersal characteristics are highly beneficial to fungi characterized by an uneven distribution of mating types. For example, mycophagy on heterothalic species increases the probability that two spores of different sex germinate near each other so that a monosporic mycelia can copulate to form a fertile mycelium of binuclear cells. Evolution of the dikaryon, parasexuality, and mating types have made possible the success of fungi as a group. It is through effective spore and mycelial dispersal, in which slugs play a significant role, that successful germination, penetration, and host colonization occur.

In summary, Ariolimax perferentially feeds on fungi which, in general, provide a food resource that is abundant, nutritious, and more readily assimilated than other available food. Additionally, Ariolimax and other slugs select the hymenium whose tissues exhibit the least mechanical barriers to feeding while simultaneously possessing the highest nutritional content of all fungi structures. Benefits to fungi of slug mycophagy probably include induced and/or improved germination of spores through digestive processes and a benign fecal innoculum, directional dispersal of propagules, and increased opportunity for genetic recombination and outbreeding.

Comparison of Sporocarps and Vascular Plant Fruits

The most interesting aspect of this study was the observation of a striking parallel between the development of sporocarps in fungi and the ripening of fruit in higher plants, and mycophagy in slugs and frugivory in birds and mammals. The dispersal of spores by air is the prime function attributed to the sporocarps of epigeous fungi (Ingold, 1953). My study, however, suggests that animal dispersal may be equally important. Sporocarps are essentially morphologically and physiologically analogous to vascular plant fruits in that sporocarps protect developing spores (*i.e.*, unicellular seeds) from drying out, defend against premature predation by molluscs (and probably also arthropods and mammals), and attract animal dispersers to mature forms by producing attractants and inactivating defensive mechanisms.

In addition, phenological changes (including exposure and availability of the highly nutritious spore-bearing hymenium; a rise in palatability, most likely attributable to a change in toxicity; and exudation of secretions and production of strong odors that frequently characterize fungi growth and development) suggest that sporocarp evolution represents an adaptation to animal as well as air dispersal. Similar morphological and physiological characteristics in hypogeous fungi, which exhibit no mechanisms for discharging spores above ground, have been considered traits that encourage mycophagy and facilitate dispersal (Ingles, 1947; Fogel and Trappe, 1978; Maser, Trappe, and Nussbaum, 1978).

In conclusion, it must be noted that the comparison of fungi sporocarps with vascular plant fruits are currently speculative since they depend on limited data, especially with respect to fungal metabolites. Nevertheless, this paper does provide information and support that can be more extensively analyzed to detect the mutually beneficial aspects of mycophagy and fungal reproduction and dispersal.

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APPENDIX A
INDEX TO VASCULAR PLANTS

Family	Genus, Species, Authority
Aceraceae	*Acer circinatum* Pursh
Berberidaceae	*Berberis nervosa* Pursh
Betulaceae	*Alnus rubra* Borg.
	Alnus rugosa (Du Roi) Spreng
Caprifoliaceae	*Linnaea borealis* L.
Ericaceae	*Gaultheria shallon* Pursh
	Vaccinium deliciosum Piper
Fumariaceae	*Dicentra canadensis* (Goldie) Walp.
Liliaceae	*Trillium recurvatum* Beck
Pinaceae	*Pseudotsuga menziesii* (Mirbel) Franco
	Tsuga heterophylla (Raf.) Sarg.
Polypodiaceae	*Polystichum munitum* (Kaulf.) Presl
	Pteridium aquilinum (1.) Kuhn.
Rosaceae	*Prunus emarginata* (Dougl.) Walp.

APPENDIX B
INDEX TO FUNGI

Family	Genus, Species, Authority
Ascomycetes	
Helvellaceae	*Helvella lacunosa* Fr. *Morchella esculenta* Pers. ex St. Adams
Basidiomycetes	
Amanitaceae	*Amanita silvicola* Kauff. *Amanita muscaria* (Fr.) S.F. Gray
Boletaceae	*Boletus mirabilis* Murr. *Boletus zelleri* Murr. *Suillus lakei* (Murr.) Smith and Thiers
Cantharellaceae	*Cantharellus cibarius* Fr.
Coprinaceae	*Coprinus atramentarious* (Bull. ex Fr.) Fries
Cortinariacea	*Cortinarius* sp.
Russulaceae	*Lactarius aurantiacus* (Fr.) S.F. Gray *Lactarius sanguifluus* (Paulet ex.) Fr. *Russula cascadensis* Shaffer *Russula emetica* (Fr.) Pers. *Russula* sp. *Russula obscuratus* *Russula pologonia* Niolle *Russula placata* Burl.
Tricholomataceae	*Armillariella mellea* (Vahlex Fr.) *Collybia* sp. *Laccaria amethystina* (Bolt. ex Hooker) Murr. *Laccaria laccata* (Sop. ex Fr.) Berk. and Br. *Lyophyllum multiceps* Peck *Marasmius oreades* (Bolt. ex Fr.) Fr. *Mycena haemotopus* (Fr.) Quel.
Strophariaceae	*Naematoloma fasciculare* (Huds. ex Fr.) Karst
Gastromycetes	*Phallus impudicus* Pers.

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THE USE OF COTTON STRIPS IN A MICROCOSM STUDY OF THE ENERGY COST OF A PREDATOR-PREY RELATIONSHIP

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INTRODUCTION

It has been stated (Macfadyen, 1963) that a major role of the soil fauna is to increase the rate of litter decomposition in the soil by stimulating microbial activity. Standen quoted in Heal et al. (1975) states that decomposition is 1.35 times higher when enchytraeid worms are present. The loss in tensile strength of cotton cloth buried in the field (Latter and Howson, 1977) has been used to compare relative rates of decomposition (Heal et al., 1975). Springett (1979) showed that under field conditions a reduction in the species diversity of soil microarthropods is correlated with a reduced rate of decomposition as indicated by loss in tensile strength of cotton strips. This same technique has been extended for use in laboratory microcosms where the effects of changing the species composition of the microarthropod fauna can be measured under controlled conditions.

METHODS

Microcosm chambers were made from soil extract agar plants sprinkled with a thin layer of fine soil (Springett, 1964). The soil was not sterilized and had been treated only by thorough mixing and the removal of those organisms which could be seen under 40x stereo-magnification. Each microcosm possessed a complement of microbial life and it was assumed that the fungi, yeasts, bacteria and protozoa were evenly distributed throughout the 60 replicates of the experimental treatments. All the microcosms were kept at constant 20°C in a saturated atmosphere during the experiment.

The experimental treatments were:

1. microcoms containing breeding populations of the collembolan Folsomia candida Willem
2. microcoms containing breeding populations of F. candida and a predator, an unidentified mesostigmatid mite (Neoparasitidae).
3. microcosms without added microarthropods.

F. candida is a generalized detritus feeder whose gut contents in the microcosms usually consist of: recognizable plant and fungal debris, amorphous dark material and small mineral particles. The adult mesostigmatid mite feeds on all life stages of *F. candida* in the microcosms and the juvenile mite on the eggs and the newly hatched collemboles.

The relative rates of energy flow in each experimental treatment were estimated by measuring the loss in tensile strength of small strips of cotton cloth, such loss being related to the degree to which the cellulose had undergone decomposition during the 41 da of the experiment. This method estimates the comparative average rates of energy flow over a period of time covering the full life cycle of the organisms. The animals were introduced into the microcosms, and after the first collembolan eggs had hatched the resulting juveniles were allowed to grow to breeding size (44 da) before the initial cotton strips were replaced by new ones and the experiment started. Throughout the experiment the microcosms contained between 100 and 150 individual of *F. candida* (excluding eggs) and an average predator population of 4 individuals.

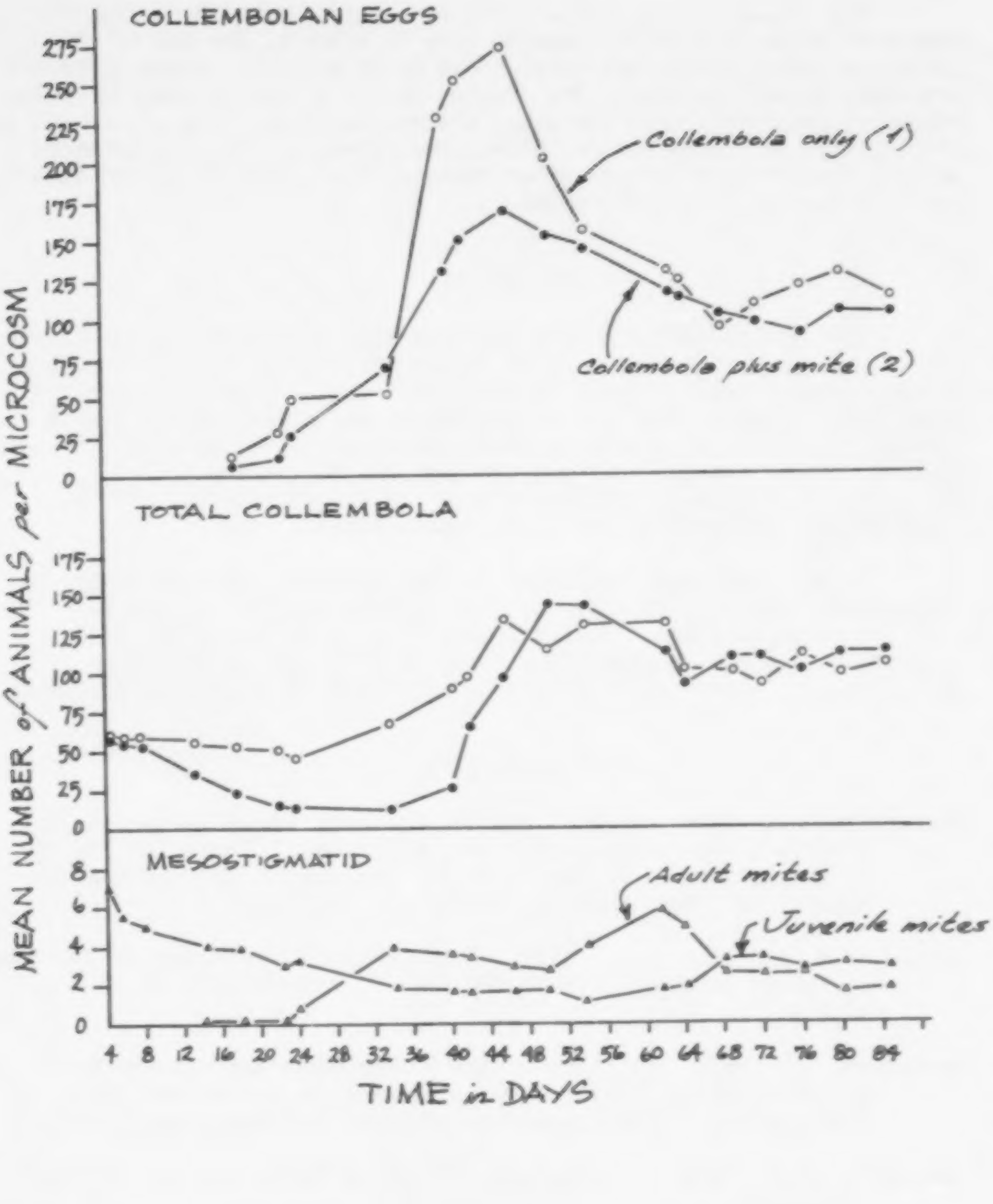
Three cotton strips of a standard size (10 wasp threads by 50 weft threads) were placed on the surface of the agar in each microcosm. After 41 da the cotton strips were removed and stored at 50% humidity and 20°C for 24 hr before the tensile strength was measured. Measurement of the tensile strength of subsamples of the cloth at the beginning of the experiment and on the strips from the microcosms were made using an Instron Tensile Testing Instrument with a strain rate of 5 cm/min, a chart speed of 10 cm/min and a full chart load of 10 kg. The results are expressed as mean kilogram load per cotton strip and as percentage loss in strength (Table 1).

TABLE 1. THE TENSILE STRENGTH AND PERCENTAGE LOSS IN STRENGTH OF COTTON STRIPS IN SOIL MICROCOSMS

Mean initial strength of cotton cloth = 1.47 kgms per strip (S.E. = 0.2)

Treatment of microcosm	mean strength (kgm/strip)	% loss in strength
	n = 60	
1. *Folsomia candida* only	0.40 S.E.=0.05	73
2. *F. candida* plus	0.27 S.E.=0.03	81
3. No microarthropoda	0.55 S.E.=0.07	63

Figure 1: PREDATOR-PREY RELATED TO TIME AND MICROCOSM



RESULTS

Figure 1 shows the mean number of eggs and total F. candida per microcosm and the mean number of adult and juvenile mites per microcosm and Table 1 the decomposition of the cotton strips in the microcosm.

The results in Table 1 and Figure 1 show that with no significant difference in average standing crop of animals, the use of the cellulose energy source was accelerated by 8% when the system contained predators as well as prey. The grazing action of the collembola on the microbial population also increased the decomposition rate of the cotton cloth (10%), but these sets of microcosms cannot be directly compared because the collembolan population represents an addition to the standing crop biomass of the microcosm.

CONCLUSIONS

This work provides direct evidence that increasing the diversity within the same physical limits increases the flow of energy through a system. When a trophic level is added to a system then the trophic level below it is called upon to provide an additional energy supply without itself having access to more resources. To do this it increases its own rate of energy flow implying that the faster energy flows through a trophic level the more frequently system excesses (Wiens, 1973) became available to the next trophic level.

Under controlled conditions in the laboratory changes in the decomposition rate of cotton strips were correlated with changes in the soil faunal populations. This suggests that it may be valid to correlate changes in the decomposition rate of cellulose in the field experiments with animal activity and in particular with species diversity.

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QUESTIONS and COMMENTS

A. MACFADYEN: Please will you elaborate on the nature of the food of Folsomia? The implication therefore is that collembolan grazing enhances microbial metabolism.

J.A. SPRINGETT: Folsomia is a generalized feeder in these cultures; the gut usually contains amorphous material, fungal hyphae and spores and small mineral particles. There were never any cotton fibers inside any of the animals we examined.

H. EIJSACKERS: Do you have any explanation for the stimulatory effect on cotton strip decomposition by Collembola after adding predators?

J.A. SPRINGETT: The collembola in the cultures with predators appeared to be much more active; at any one time more individuals were running across the agar or were actively feeding. This increased mobility may have required more energy. As the mites were preying on the collembolan population without decreasing significantly the standing crop of Collembola, presumably the production of Collembola must have been stimulated. As the cotton strip represents the energy source to the microcosm an increased energy demand should result in increased decomposition of the cotton strip.

MS. R. SNIDER: Is it possible that the size distribution varied in the Collembola populations due to the selection of certain sizes by the predator? Did you analyse the size distribution at the end of the experiment?

J.A. SPRINGETT: We did check on the size distribution as we had the impression that there were more large collemboles in the cultures without predators. There was no significant difference in the body lengths of the populations. The larger specimens in the predator-free cultures were a very dense white which may have indicated a difference in biomass or development of fat bodies, however this was not measured.

A. MACFADYEN: Are you suggesting that the microbial activity on the cotton strips is increased or are the Collembola feeding directly on the cotton fabric?

J.A. SPRINGETT: Yes, I am suggesting that feeding by

Collembola stimulates microbial activity by removing non-active colonies, by exposing new areas of cellulose for colonization and by distributing spores across the cotton strip. The Collembola does not appear to feed directly on the cotton fabric.

A NEW TECHNIQUE FOR THE ANALYSIS OF THE DIGESTIVE TRACT CONTENT IN CARABID BEETLES

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RESUME

Un des problèmes majeurs de l'Ecologie du Sol est la détermination de la place que chaque espèce occupe à l'interieur du réseau trophique. Ce problème se résoud par la connaissance du régime alimentaire des espèces de chaque niveau trophique.

Notre étude porte sur les Carabiques carnassiers inféodés à l'écosystème forestier.

Les méthodes utilisées jusqu'à présent pour déterminer le régime alimentaire exact des Carabiques sont parfois fastidieuses, et souvent peu précises. Seule l'étude du contenu des jabots d'animaux récoltés dans la nature peut donner l'image exacte du régime alimentaire. Malheureusement, pour les carnassiers, l'identification des débris dans le tube digestif est fort difficile. La méthode que nous proposons est basée sur la reconnaissance de ces débris au Microscope Electronique à Balayage. La comparaison du tégument et des fragments de phanères trouvés dans les jabots avec ceux d'animaux capturés dans le biotope originel des Carabiques permet la détermination précise des proies. La précision de cette méthode peut aller jusqu'à la détermination au niveau spécifique.

Ground beetles are well known predaceous Coleoptera. In fact most of them mostly eat animal prey; and numerous carabids are uniquely carnivorous. However, this is not true for all of them: they also often accept feeding on plant tissues, sometimes partially, sometimes totally. LINDROTH observed as soon as 1949 entirely phytophagous carabid beetles. Thus, these beetles can potentially constitute crop pests.

Thus, there was a dilemna concerning the actual role these animals play in an ecosystem. Are they to be considered as deleterious pests? Or are they to be considered as effective predators and then eventually utilised in biological pest control? In fact, the answer to both questions is yes, depending on the species considered. The question thus remaining is to determine the exact place each species occupies in the trophic network, i.e. the diet of each species.

According to the literature, forest ground beetles are mainly carnivorous, while phytophagous Carabids are found in open land. This probably explains why the bulk of the studies on Carabids diet is concerned with field carabids. The use we can make of the animals firstly depends on the width of the prey spectrum. In fact, a predator which is a specialistis so dependent upon its prey that it can hardly regulate the prey population. On the contrary, a generalized predator, when able to switch from one prey to another would more effectively limit increases in population.

Most of the species actually investigated show a broad spectrum of prey. For example, SKURAVY studied the crop content of 12 field species. She found that *Pterostichus*, *Harpalus*, *Agonum* and *Calathus* preyed upon at least 18 different families of Arthropods: Arachnida, Formicoïdea, Aphidoïdea, Curculionidae... *Pterostichus cupreus* chose its preys among 14 of these different families, while *Harpalus aeneus* preyed upon only 4. Thus, *P. cupreus* has the widest spectrum of prey among the *Carabidae* SKURAVY studied. KABACIK-WASYLIK observed that *P. cupreus* also ate eggs and dead animals. From these results, *P. cupreus* is at the same time a scavenger, a primary consumer, a secondary and a tertiary consumer: a true case of generalisation. Opposite to this example are oligophagous species of Carabidae: they exist, but are very few in number compared to generalized species. They have not formely been described among the forest dwelling species.

In her work, SKURAVY did not determine the prey from crop content more precisely than the family level; this is true also for nearly all authors, and is due to the method used: the technique consists of dissecting the digestive tract, displaying its content on micro-slides and observing with a photonic microscope. Thus the identification of prey is done from prey fragment. It is thus possible only when the pieces are parts of appendages, heads, etc, or recognizable organs. In such a situation, it is practically impossible to recognize at more than merely the family level.

Some authors succeeded in determining some prey species of certain Carabids. ERNSTING demonstrated

Notiophilus biguttatus preyed upon the Collembolan *Orchesella cincta* and *Tomocerus minor*. However these were laboratory experiments: ERNSTING gave previously identified Collembola to *N. biguttatus*. Such observations do not prove that these *Collembola* are natural prey; they only demonstrate the possibility. Therefore analyses of the contents of the digestive tract are necessary on animals captured in their habitat.

The extraction of the contents of the digestive tract must be done from the anterior part of the tract. Further posterior the meal will be digested and pieces will be unrecognizable. In the case of Carabid beetles, this means the extraction must be done when the meal is between the mouth and the proventriculus, i. e. in oesophagous and crop. In fact, one can find there the most recognizable fragments.

When dissecting, one will notice that the crops are either full of solid items, or full of liquid items, or sometimes empty, depending on the species dissected. Thus, solid items are never observed for example in the *Carabus* group, the crop of which, if full, only contains liquid. This is due to its type of food uptake: extraintestinal digestion. Up to now only one process of digestion has been described in ground-beetles. According to this process, three types of Carabidae are distinguishable: those with totally intraintestinal digestion, those with exclusively extraintestinal digestion, and those with intraintestinal and extraintestinal digestion.

It is thus very clear that visual analyses of crop content are hampered by extraintestinal digestion, although it is the most generally used method. In spite of these difficulties, the visual method for analysing crop contents must be maintained for at least two reasons:

1) It is the only available method providing statistical data;

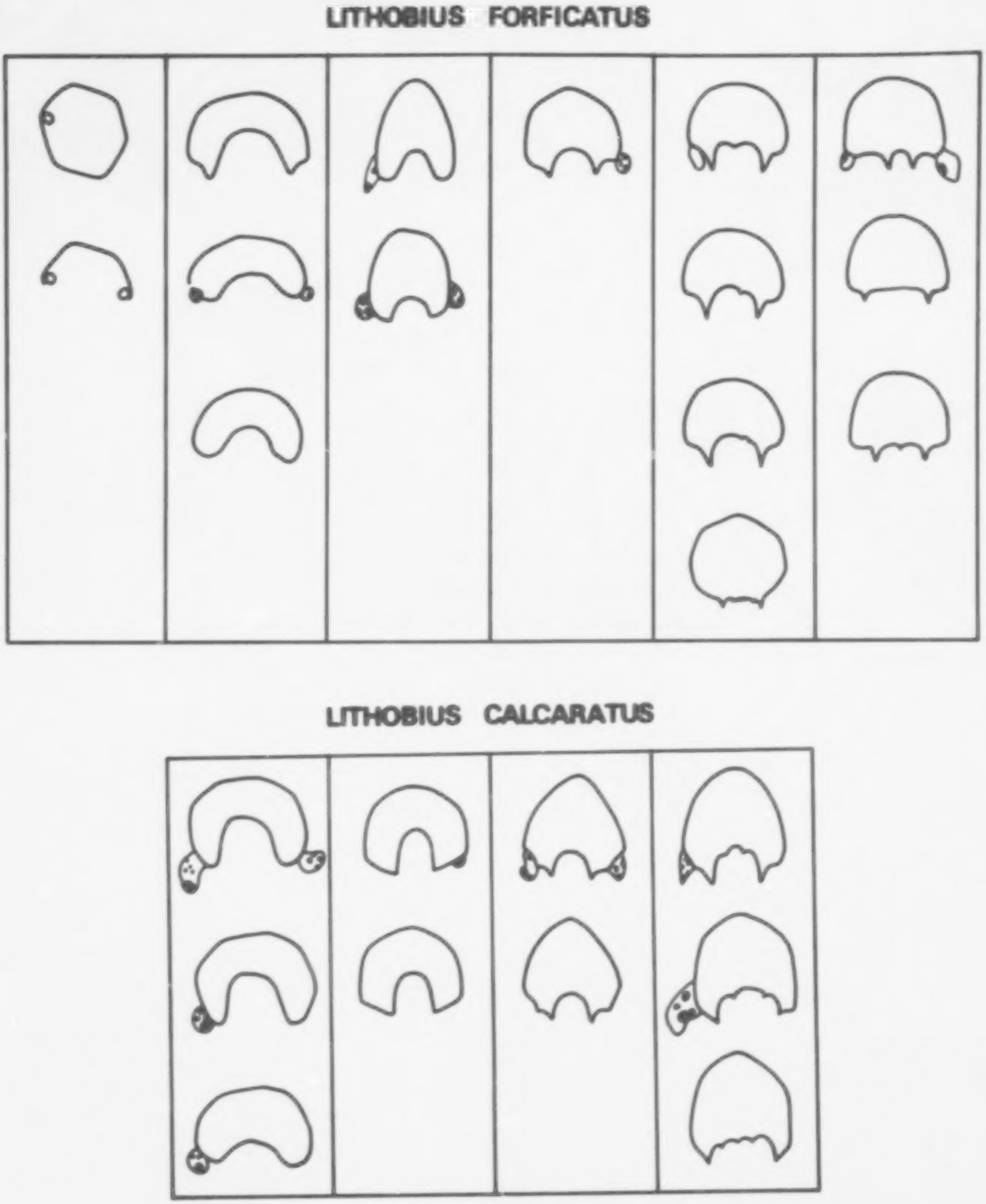
2) the crop contains the only available information for the identification of natural prey.

In fact every prey fragment in the crop is a piece of dietary information. However, untill recently, these very small fragments could not be precisely utilized, unless they were recognizable organs. That is why we have devised a new method for the identification of natural prey from the very small prey fragments contained in the crop. This method consists of the observation of these fragments with a Scanning Electron Microscope.

In a full crop, numerous fragments of unidentifiable organs are observable, which lack a particular shape, size or feature recognizable as belonging to a given prey species. These fragments can only be identified as belonging to one or more Arthropods. At a greater magnification the epicuticular relief is observable: setae, spines, pores, ... the exact shape of which is not actually observable with another technic than S.E.M. Fig.1 show some spines which differ in size, shape and density. The question remains to correlate each type of spine to one species of Arthropod. Is this "micromorphology" species characteristic? It certainly is if we refer for example to the colors of some Insects cuticule: these specific colorings are due either to pigments or to peculiar epicuticular microsculptures. To prove this point of view, we observed two species of the same genus: *Lithobius calcaratus* and *Lithobius forficatus*. Table 1 gives a list of pertinent features, i.e. those features from which it is possible to distinguish *L. calcaratus* from *L. forficatus* and vice-versa.

The body and appendages of both these Lithobius are covered with a kind of scale on nearly all the surface. *L. calcaratus* has rippled pseudoscales while *L. forficatus* has dotted pseudoscales. These microsculptures are also found on the bases of the sensilla trichodea. The posterior hedge of the pseudoscales generally bears some little spines: the length of which is variable. The longest spines are observed on the pseudoscales of *L. forficatus*.

The surface of the setae of every sensilla, whatever its length is, are very much alike in the two species: they all are grooved and the grooves may twist round the setae. It is thus remarkable how similar the sensilla are all over the body and in both species, the only difference being their bases. In fact, the setae bases vary a lot in shape both when comparing two setae bases of one individual and when comparing the setae bases of the two species. All the setae bases are protuberant except one type which is flat: this type is only found in *L. forficatus*. The setae bases are crescent shaped well marked in *L. calcaratus*, while more discreet in *L. forficatus*; in the latter species some bases have the shape of a semi-circumference and some others are nearly round. In both species the setae bases bear generally two big spines and often more or less numerous little ones. Their shape, number and position vary from a species to the other: fig. 2; are the diagram of the most frequently observed setae bases. In both species the sensilla trichodea are generaly accompanied by one or two secretory gland the pore of which are seen at each side of their base. At last, similar sensilla placodea are observed in both species.


LITHOBIUS FORFICATUS

LITHOBIUS CALCARATUS

FIGURE 2 . Variations of the form of setae bases

FIGURE 3 . Lithobius forficatus :

1 : sensilla trichodea;
2 : general view of pseudoscales;
3 : pit on pseudoscales;
4 : sensilla placodea;
5-13 : setae bases of sensilla trichodea.

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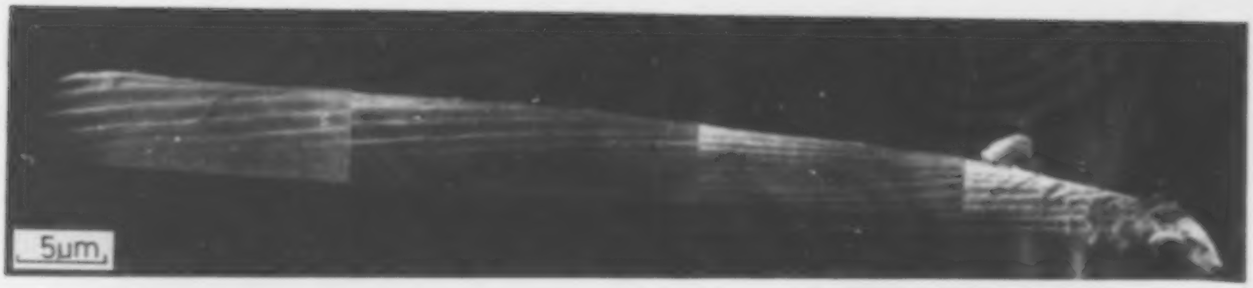

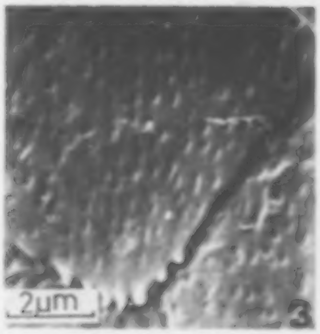

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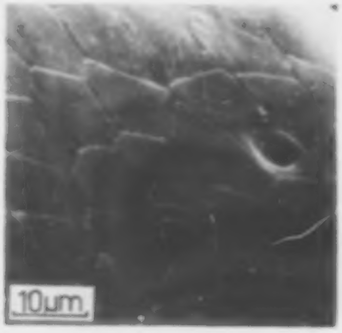

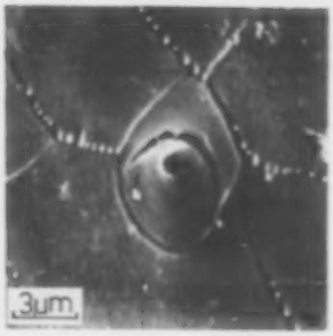

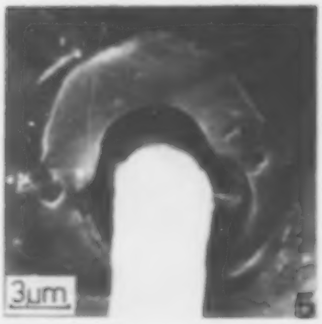

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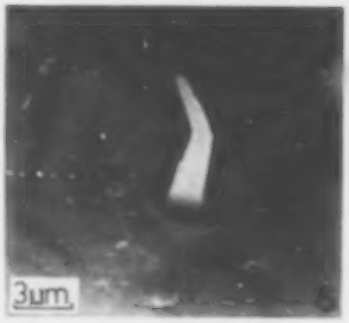

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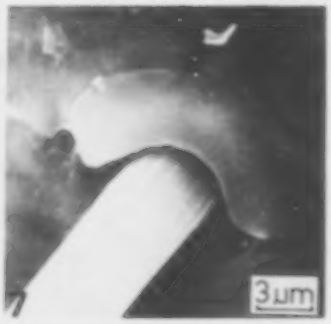

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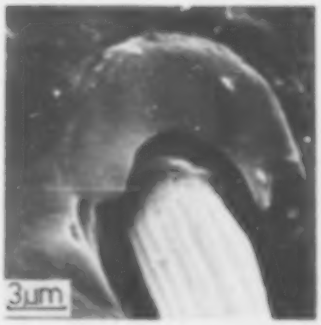

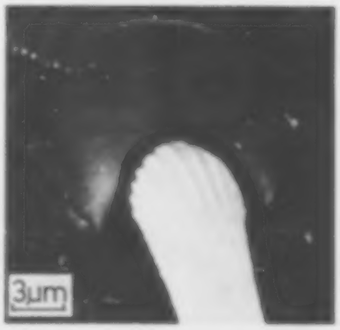

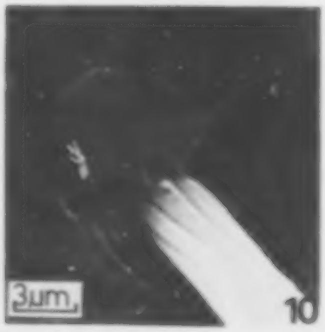

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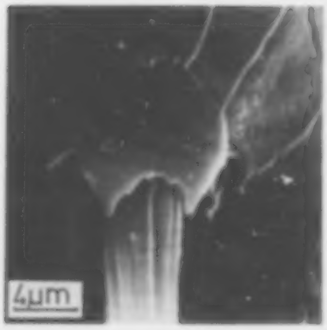

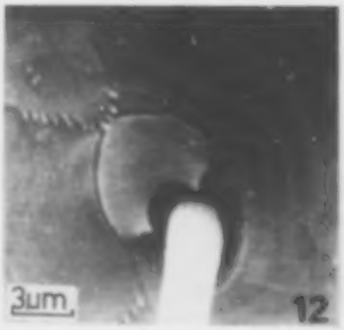

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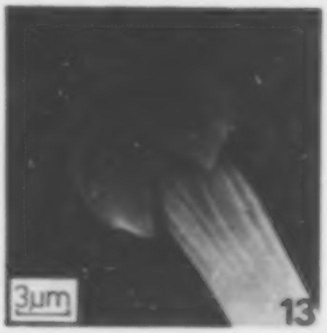

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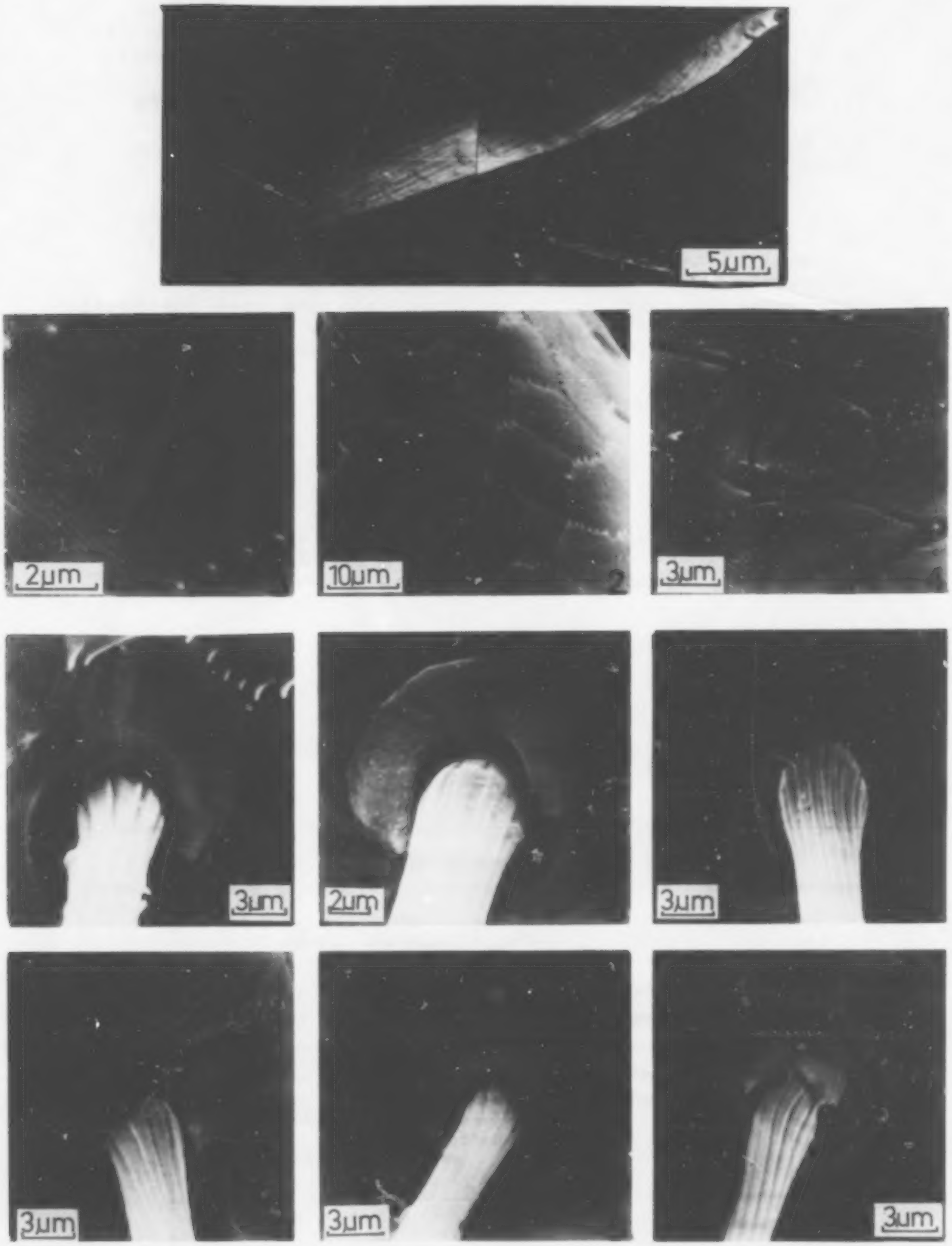
FIGURE 4 : Lithobius calcaratus :

1 : sensilla trichodea;
2 : general view of pseudo scales;
3 : ripple on pseudoscales;
4 : sensilla placodea ;
5-10 : setae bases of sensilla trichodea.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To summarize this comparison, it appears clearly some similarities in both *Lithobius*: sensilla placodea, setae, pseudoscales; those similarities correspond to the fact both *forficatus* and *calcaratus* belong to the genus *Lithobius*. However there exist some differences, the structure of the pseudoscales and the structure of the setae bases. Those differences, observable only with a S.E.M., are enough to distinguish one species from the other, even from very small pieces.(Fig. 3 and Fig. 4)

To conclude we shall just ask one question: why has this micromorphology never been used up to now by systematicians? The reason was probably there was no interesting aim. Which new information would this micromorphology afford? None if we only are soil zoologist. But if we are soil ecologist, we have now an attractive aim: the analysis of crop content of naturally captured predators.

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ACKNOWLEDGMENTS

We would like to thank Mrs. Munoz and Mrs. Vannier and Miss Munsch for typing and preparing the figures.

TABLE 1 . Caracteristic features of species of Lithobius

		LITHOBIUS CALCARATUS	LITHOBIUS FORFICATUS
scale	plane surface	ripple	pit
	hedge spine	short	long
Sensilla trichodea	seta	groove	groove
	base	ripple 0 or 2 to n tips 0 or 2 glandular pores	pit 0 or 2 tips more or less distant 0 or 2 glandular pores
Sensilla placodea		yes	yes

THE GEOPHAGOUS EARTHWORMS COMMUNITY IN THE LAMTO SAVANNA (IVORY COAST): NICHE PARTITIONING AND UTILIZATION OF SOIL NUTRITIVE RESOURCES

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The few descriptions of earthworm communities available from tropical grasslands clearly show dominance of the geophagous species. This has particularly been verified in the tropical pastures of Laguna Verde (Vera Cruz, Mexico) (LAVELLE, MAURY and SERRANO, 1979), in the north Guinean savannas of Foro-Foro (Bouaké, Ivory Coast) (LAVELLE, unpublished) and in the south Guinean ones of Lamto (Toumodi, Ivory Coast) (LAVELLE, 1978) (Table 1). In the first locality, almost the entire community is composed of geophagous earthworms. In the Lamto savannas, the herbaceous facies are also stocked with a great majority of geophagous (97%) whereas the shrub facies (89.2%) and the savanna which has been unburned for 12 years (69.7%) which has a thick shrub cover, have more diversified communities. At the Foro-Foro station, 230 km north of Lamto, the savanna is rather thickly covered with shrubs and 77.8 to 88.1% of the earthworm biomass is made of geophagous individuals. On the contrary, temperate grasslands stocked whith *Lumbricidae* have few geophagous worms : 13.1% of the total biomass in a French pasture (BOUCHE, 1975).

TABLE 1. Trophic structure of some earthworm communities in tropical and temperate grasslands (in % of total biomass).

Locality	Vegetation type		Geophageous	Detritivorous	Authors
Laguna Verde (Vera Cruz, Mexico)	Secondary pasture		≃ 100	ε	LAVELLE, MAURY and SERRANO, 1979
Foro Foro (Bouaké, Ivory Coast)	North guinean savannas	*Parenari* savanna	88.1	11.9	LAVELLE, unpublished
		Lophira savanna	77.8	22.2	
Lamto (Toumodi, Ivory Coast)	South guinean savannas	grass savanna	97.0	3.0	LAVELLE, 1978
		shrub savanna	89.2	10.8	
		unburned savanna (12 years)	69.7	30.3	
Citeaux (Dijon, France)	Permanent pasture		13.1	86.1	BOUCHÉ, 1975

This dominance of geophagous populations seems to be a general characteristic of tropical grasslands. It is, therefore, important to know their community structure and how they feed on the soil, in order to understand their general function. Four years of field observations in the Lamto savanna and laboratory experiments focus on this question.

NICHE PARTITIONING IN THE EARTHWORM COMMUNITIES OF THE LAMTO SAVANNAS

The earthworm communities of Lamto savannas are made up of eight principal species ; six are Megascolecidae : *Dichogaster agilis, D. terrae-nigrae; Millsonia anomala, M. lamtoiana, M. ghanensis and Agastrodilus opisthogynus* ; the two others are Eudrilidae : *Chuniodrilus zielae* and *Stuhlmannia porifera.*

Their ecological niches can be defined with six principal variables. Three of them describe the spatiotemporal niche : vertical distribution of populations in the soil, horizontal distribution in the mosaïc drawn up by the different vegetal facies (herbaceous or shrub savannas, burnt or unburnt patches) and the seasonal cycle of abundance (Fig.1). The three other variables represent the trophic dimension of the niches : species size, demographic profile, and energetic value of ingested food (Table 2).

TABLE 2. Trophic niche of the different species of earthworms in the Lamto savannas.

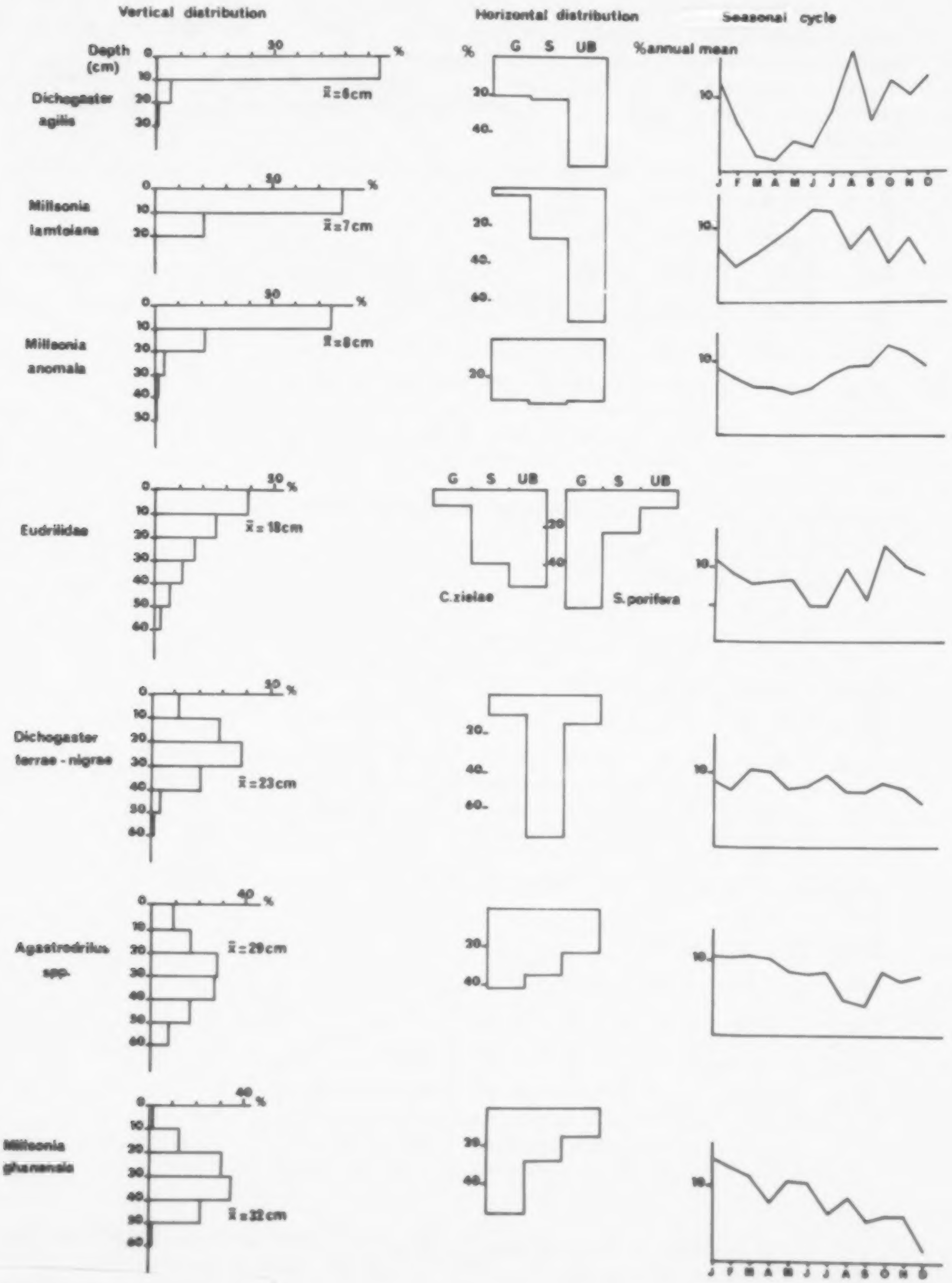
Species	Maximal weight (g)	Food	Energetic value of food in Kcal/g	Demographic index
D. agilis	0.60	litter	≃ 4,000	200
M. lamtoiana	32.0	litter	≃ 4,000	17
M. anomala	6.0	soil (0-10cm)	90	50
D. terrae-nigrae	28.0	soil (10-30 cm)	50	4.5
Eudrilidae	0.25	soil (0-30 cm)	150	200
M. ghanensis	16.0	soil (10-40 cm)	40	2.9
A. opisthogynus	4.0	soil (20-40 cm) + Eudrilidae ?	?	4.9

The index ($D = 10^3 \frac{F}{C.E_v}$) combines different elements of the demographic profiles : adult fecundity (F), duration of the growth period until maximum weight (C), and life expectancy of young hatchling (E_v) (LAVELLE, 1979).

Spatiotemporal niche overlap has been estimated with the Ojk index of PIANKA (1974) along each of these previously mentioned three axes (Table 3).

Seasonal cycles have high overlap ratios (0.72 to 0.95 with a mean value of 0.90). Thus, niche separation is mainly realized through the colonization of different savanna facies (Ojk = 0.13 to 0.96 ;

FIGURE 1. Main constituants of the Lamto's earthworms spatiotemporal niches. G = grass savanna, S = shrub savanna, UB = unburned.



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$\overline{Ojk}$ = 0.70) and the occupation of the diverse layers of the soil (Ojk = 0.06 to 0.93 ; $\overline{Ojk}$ = 0.47).

TABLE 3. Spatiotemporal niche overlap (Ojk index) in the earthworms communities of Lamto savannas (D.a. : *Dichogaster agilis* ; M l. : *Millsonia lamtoiana* ; M.a. : *Millsonia anomala* ; D.t. : *D. terrae-nigrae* ; Eu. : *Eudrilidae* ; C.z. : *Chuniodrilus zielae* ; S.p. : *Stuhlmannia porifera* ; A.o. : *Agastrodrilus opisthogynus* ; M.g. : *M. ghanensis*).

A. Vertical distribution

M.l.	0.93					
M.a.	0.91	0.96				
D.t.	0.11	0.44	0.49			
Eu.	0.38	0.48	0.62	0.57		
A.o.	0.08	0.10	0.27	0.33	0.91	
M.g.	0.02	0.05	0.24	0.29	0.77	0.88
	D.a.	M.l.	M.a.	D.t.	Eu.	A.o.

B. Horizontal distribution

M.l.	0.95						
M.a.	0.73	0.89					
D.t.	0.13	0.55	0.74				
C.z.	0.94	0.53	0.79	0.75			
S.p.	0.54	0.95	0.82	0.47	0.41		
A.o.	0.76	0.56	0.97	0.71	0.72	0.92	
M.g.	0.64	0.37	0.89	0.55	0.53	0.95	0.96
	D.a.	M.l.	M.a.	D.t.	C.z.	S.p.	A.o.

C. Seasonal cycle

M.l.	0.80					
M.a.	0.94	0.91				
D.t.	0.84	0.92	0.95			
Eu.	0.93	0.87	0.93	0.94		
A.o.	0.82	0.91	0.92	0.99	0.95	
M.g.	0.80	0.89	0.91	0.94	0.87	0.95
	D.a.	M.l.	M.a.	D.t.	Eu.	A.o.

A matrix of results has been established after multiplication of the calculated values as the three variables seem to be independent (PIANKA, op. cit.) (Table 4).

TABLE 4. Total spatiotemporal niche overlap.

	D.a.	M.l.	M.a.	D.t.	C.z.	S.p.	A.o.
M.l.	0.71						
M.a.	0.62	0.65					
D.t.	0.01	0.21	0.34				
C.z.	0.33	0.40	0.46	0.40			
S.p.	0.19	0.11	0.47	0.25	0.41		
A.o.	0.04	0.05	0.24	0.23	0.62	0.79	
M.g.	0.01	0.02	0.18	0.15	0.36	0.64	0.80

Though the total spatiotemporal niche overlap (Ojk = 0.01 to 0.80 ; $\overline{Ojk}$ = 0.35) is low among most of the species, a good ecological separation is evidently indicated. Two groups of species however appear rather close in this spatiotemporal space (Fig. 1). *D. agilis, M. lamtoiana* and *M. anomala* inhabit the upper layers and prefer burnt or unburnt shrub savannas. On the other hand, *A. opisthogynus, M. ghanensis* and the Eudrilidae (*C.zielae* and *S. porifera*) are deep soil dwellers, characteristic of the open savannas.

Nevertheless, the examination of trophic niches shows that those species whose spatiotemporal niches are similar are in fact distinctive in that they exploit their resource in different manners. The distribution of species in the trophic space has been figured using orthogonal axes -as it is easier to represent- despite the fact that the variables are certainly more or less linked (LAVELLE, 1979)(Fig. 2).

Detritivorous species are clearly separated from the others because of the high caloric value of the litter that they ingest. *D. agilis* is small with a high demographic index. *M. lamtoiana* is large and its populations turn over is not so high. Among the geophagous species, small ones are distinctive in that they feed on relatively rich soil and have a high demographic index (the two Eudrilidae : *C. zielae* and *S. porifera)*; there are also two large species with a low demographic index and poor food (*D. terrae-nigrae* and *M. ghanensis*) and an intermediate one, *M. anomala. A. opisthogynus*, whose exact diet is not known, has not been figured here. Some recent indications could show that this species is partly carnivorous and feeds on Eudrilidae.

After combining the two niche spaces, the separation is clearly the consequence of rather high specialization. This permits the five main geophagous species to exploit well-separated compartments of the ecosystem. Vertical distribution makes great differences : *M. anomala* exploits the upper layers of the soil, unlike *M. ghanensis* and *D. terrae-nigrae* which are deep dwelling species. It is difficult to study individually the vertical distribution of the two species of Eudrilidae as the young cannot be distinguished. Nevertheless, some indications show that *C. zielae* is more limited to upper strata, as is *M. anomala* whereas *S.porifera* could be a deep dwelling worm.

FIGURE 2. Representation of Lamto's earthworms trophic niches. Wx : maximum weight of the species ; D : demographic index (F : adult fecundity, C : total length in months of growth period until maximum weight, E_v : life expectancy of young at birth in months) Q : energetic value of the ingested food in kcal/g dry weight).

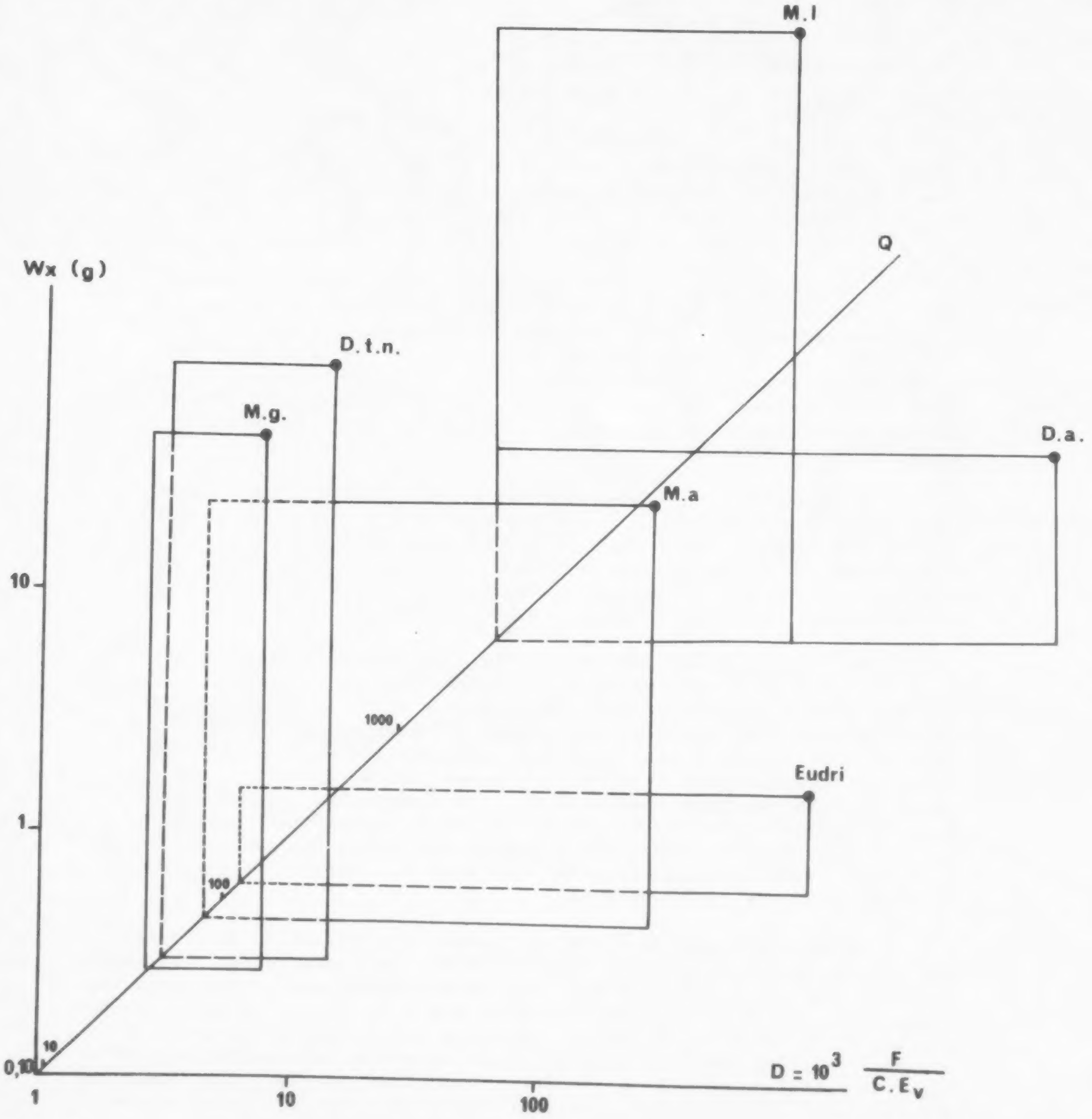
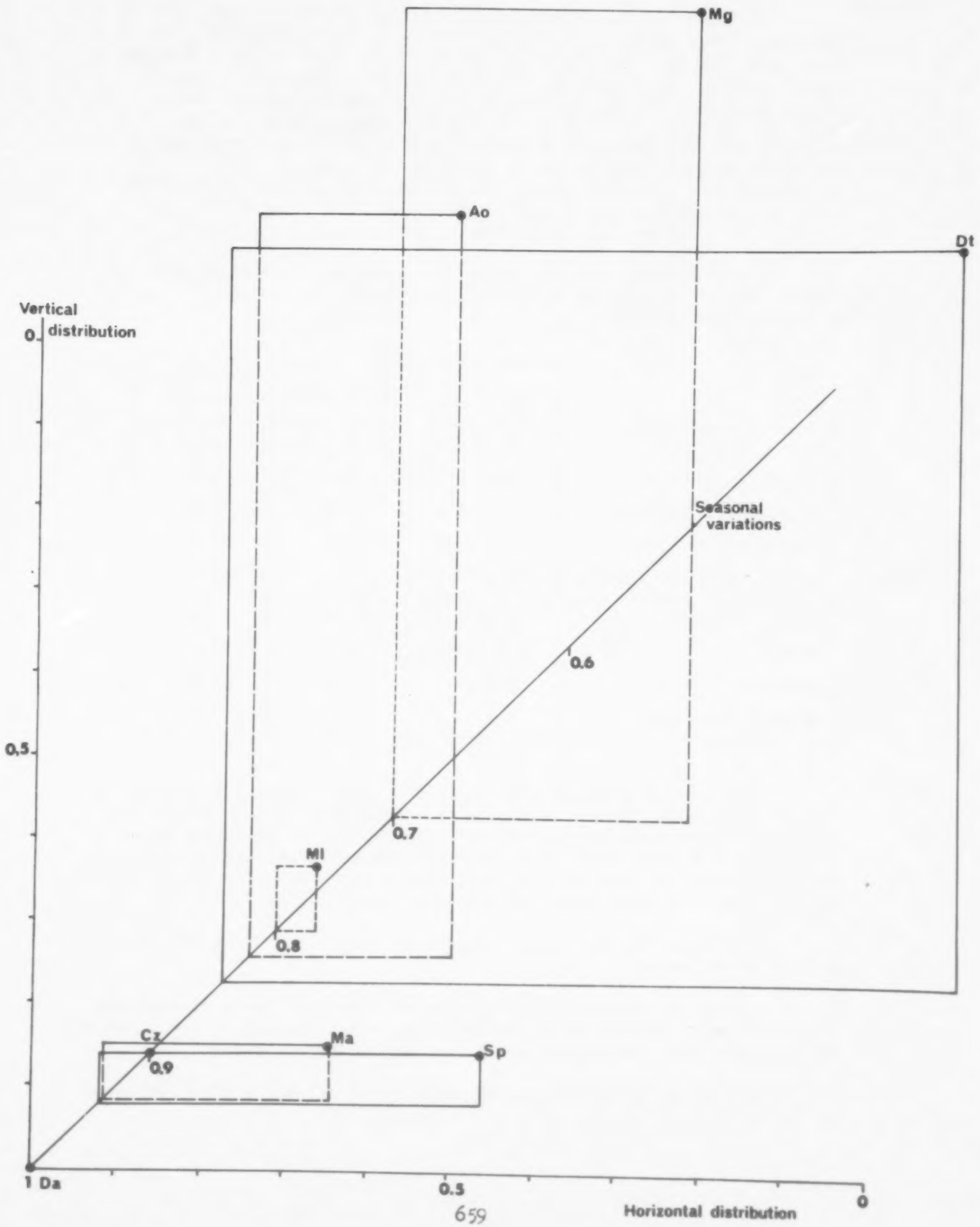


FIGURE 3. Representation of Lamto's earthworms spatiotemporal niche overlap coefficients (Pianka's Ojk) in the space of the three principal axes.



M. anomala and the eudrilid *C. zielae* differ in size, and, therefore, they exploit the environment in different manners ; the first one, a quite large species, demonstrates no preference for the organic content of the soil, while the second, thanks to its small size, ingests only soil enriched in organic matter. Indeed Eudrilidae can more easily feed on low organic matter concentrations (decomposed rootlets and surface organic film), and they do not ingest the large sandy particles. The composition of casts of these two taxa demonstrates this difference and confirm the tendency of *M. anomala* to be generalists while Eudrilidae appear more specialized, using the soil in a "coarse grained manner" (Table 5).

TABLE 5. Granulometric composition and main characteristics of organic matter in casts of *M. anomala* and Eudrilidae and control soil in a herbaceous savanna.

	Control soil (0-40 cm)	Eudrilidae	*Millsonia anomala*
Clay < 2 µ	3.3 - 3.7	5.0	5.2
Fine silt 2-20 µ	5.7 - 6.5	7.3	8.6
Coarse silt 20-50 µ	7.5 - 8.5	12.0	11.5
Fine sand 50-200 µ	25.5-29.0	40.0	27.0
Coarse sand 200-2,000 µ	50.5-56.5	32.0	46.5
C ‰	1.9 - 8.2	10.1	5.8
N ‰	0.17-0.57	0.76	0.57
C/N	10.8-15.3	13.3	10.2
Organic matter %	0.6 - 1.4	1.7	1.0

The two large geophagous species *M. ghanensis* and *D. terrae-nigrae* have close trophic niches ; the separation is made by a different vertical distribution and the colonization of different patches of savanna : *M. ghanensis* prefers the sandy soils of herbaceous savannas whereas *D. terrae-nigrae* is more likely to be found in the more clayey and better drained soils of the burnt shrub facies.

The structure of these communities raises two questions that we have tried to answer.

1. Is the vertical distribution of these species a consequence of the present competitive situation or of real adaptation, including for the deep dwelling geophagous whose food seems very poor ?

2. How do these earthworms utilize the organic matter contained in the soil ?

RELATIONS OF SOIL DEPTH WITH INGESTION AND GROWTH RATES OF GEOPHAGOUS EARTHWORMS

In order to answer the first question, we have fed individuals of the three main species (*M. anomala* young and adults, young *M. ghanensis* and *D. terrae-nigrae*) with soil taken from the different soil layers of a shrub savanna. Five layers have been distinguished, whose main characteristics appear in Table 6.

TABLE 6. Main characteristics of organic matter in the different strata of the shrub savanna soil used for earthworm cultures.

	Depth (cm)	0-1	2-5	5-10	10-25	30-40
Whole soil	Organic carbon ‰	11.8	9.8	8.3	7.0	4.1
	Total nigrogen ‰	0.58	0.50	0.40	0.30	0.30
	C/N ratio	20.40	19.5	20.8	23.3	13.6
	Total organic matter ‰	20.4	16.8	14.3	12.0	7.0
Light organic fraction	%	0.29	0.22	0.24	0.10	0.15
	C ‰	26.7	36.7	42.2	41.6	29.6
	N ‰	7.4	5.6	4.6	3.6	3.8
	C/N	3.6	6.6	9.3	11.7	7.9
Humic acids	Total fulvic acids (in C ‰)	2.53	1.91	1.57	1.54	1.36
	Total humic acids (in C ‰)	0.61	0.74	0.74	0.43	0.16
	AF/AH	4.18	2.58	2.12	3.69	8.25
	Total humic matter	3.14	2.65	2.31	2.02	1.53
	Humification coefficient	26.5	27.1	27.8	29.0	37.6

Soils characteristics

Most of the data shows a vertical gradient of the organic matter characteristics in the soil. The highest values of total organic matter content as well as total introgen, light organic fraction or total humic acids are observed in the 0-1 cm layer, decreasing more or less regularly towards depth. Total fulvic acids follow the same pattern whereas humic acids are more concentrated in the 2-10 stratum. C/N ratios of total organic matter show erratic variations, but as far as the light organic fraction is concerned, C/N increases regularly with depth. The AF/AH ratio shows rather different variations with minimum values between 2 and 10 cm.

Methods

The soil ingestion by earthworms has been measured by a method already utilized in several works (LAVELLE, DOUHALEI and SOW, 1974 ; LAVELLE, 1975) and subsequent weight variations were observed. All conditions were alike in the different cultures except for the soil origin. As many earthworms as possible have been put in cultures in order to have significant results. As a matter of fact, the growth of these earthworms does not follow a regular pattern. In the normal course of the animal's life, very intense growth periods occur followed by rest periods characterized by a no growth or even a little decrease of the weight due to a decrease of soil ingestion (LAVELLE, 1978). According to these observations, the total duration of cultures (140 to 700 worms x days in each different series) should give significant means in most of the cases despite the fact it has not been possible to establish any statistical proof.

Results

Table 7 illustrated by figure 4 gives the main results, the detail of which will be given in a further publication (SOW, to be published).

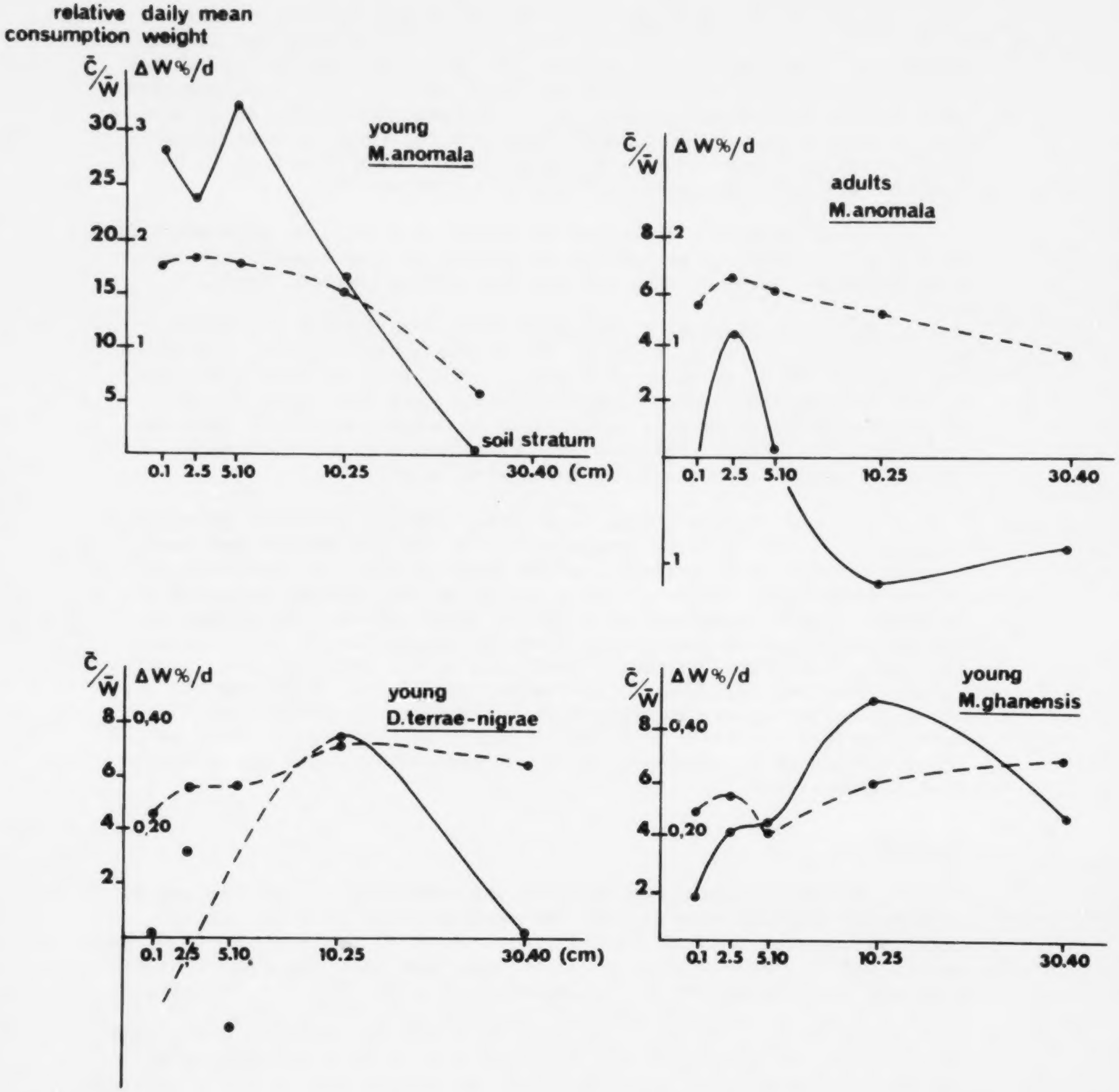
TABLE 7. Mean daily weight variations (ΔW %/day) and relative soil ingestion ($\overline{C}/\overline{W}$ in g dry soil ingested/g fresh weight/day) of three geophageous species fed with soils from different layers.

Species	Total, duration of cultures (worm x weeks)	Soil layer (cm)	ΔW %/d	$\overline{C}/\overline{W}$	$\frac{\Delta W \text{ \%/d}}{\overline{C}/\overline{W}}$
Young *M. anomala*	100	0 - 1	2.79	17.3	0.161
	100	2 - 5	2.32	18.0	0.129
	100	5-10	3.26	17.3	0.189
	100	10-25	1.65	15.1	0.110
	100	30-40	0.34	6.1	0.055
Adult *M. anomala*	30	0 - 1	-0.31	5.66	-0.055
	20	2 - 5	1.17	6.81	0.172
	20	5-10	0.11	6.07	0.018
	20	10-25	-1.24	5.53	-0.224
	20	30-40	-0.86	3.95	-0.218
Young *M. ghanensis*	64	0 - 1	0.09	5.03	0.018
	66	2 - 5	0.22	5.62	0.039
	32	5-10	0.22	4.21	0.052
	64	10-25	0.45	5.98	0.075
	81	30-40	0.23	6.67	0.034
Young *D. terrae-nigrae*	74	0 - 1	-0.01	4.16	-0.0024
	67	2 - 5	0.16	5.62	0.028
	76	5-10	-0.17	5.34	-0.032
	49	10-25	0.38	7.17	0.053
	65	30-40	0.02	6.35	0.003

This demonstrates important variations in relative soil ingestion (dry weight of daily ingested soil divided by the earthworm 's fresh weight) as well as in the animal weight changes as a function of soil depth.

Young *M. anomala* have the highest relative soil ingestion ($\overline{C}/\overline{W}$ = 17 to 18 g dry soil/g fresh weight/day) in the upper strata (0 to

FIGURE 4. Mean relative soil ingestion ($\overline{C}/\overline{W}$ in g dry soil/g fresh weight/day) and daily weight variations (%/day) of three species of geophageous earthworms fed with soil taken from different depths in a shrub savanna.



10 cm) but it decreases in the deeper layers, first slightly (15.1 in the 10-25 cm layer),then markedly (6.1 in the 30-40 cm soil). Weight variations are always positive ; they are elevated in the first three layers (2.3 to 3.3%/day), and the maximum is observed in the 5 to 10 cm stratum. In the deeper soils, poorer in organic matter, growth diminishes greatly but is never reduced to zero.

Within the same experimental conditions, adult *M. anomala* have a clear preference for the 2 to 5 cm horizon as this is the only one that allows them a significant increase in weight (ΔW%/day = 1.17). In the 5-10 cm soil their growth is very slow (0.11% day) and in the other ones, they lose weight (-0.31% in the 0-1 cm stratum, -1.24% and -0.86% respectively in the 10-25 and 30-40 strata). Soil ingestion follows similar variations , though it is somewhat decreased. It is maximal in the 2-5 cm soil (6.8) and diminishes regularly towards deeper horizons (6.1, 5.5 and 4.0 in the successive strata from 5 to 40 cm) as well as in superficial ones (5.7 in the 0-1 cm soil).

These results confirm the narrowing of ecological tolerances of adults with respect to environmental factors such as temperature and soil moisture (LAVELLE, DOUHALEI and SOW, 1974 ; LAVELLE, 1975).

Cultures of young *M. ghanensis* give very different results. Weight variations are positive in all of the soils, but they are maximum with the 10-25 cm earth (0.45%/day) while they decrease gradually in the more superficial (0.22 to 0.09%/day) ones. Soil from the 30 - 40 cm stratum still permits an increase of weight, but it is less significant (0.23%/day). Relative soil ingestion does not vary much, although it seems to increase regularly with depth.

Young *D. terrae-nigrae* show rather similar patterns. Interestingly, it is the 10-25 cm stratum that ensures the fastest and most regular growth. It is erratic, in the upper strata, and mortality is elevated. We often observe first a period of fast growth, followed by an equally rapid decrease that leads to death. Those soils richer in organic matter allow a quick but temporary growth as if some deficiency disease could appear. On the contrary, in the 10-25 stratum, growth is slow, but regular, and the mortality rate is low. Soil from the 30-40 stratum just allows earthworms to maintain their weight, ant the mortality rate is rather elevated. Relative soil ingestion shows variations similar to *M. ghanensis* as it increases slowly when given soils from deeper strata.

Conclusions

Weight variations of worms of the three studied species are dependent on the soil they ingest. The optimum depth is 2 to 5 cm for adult *M. anomala*, 5 to 10 for the immature and 10 to 25 for young *M. ghanensis* and *D. terrae-nigrae*.It can be concluded that these two last species are truly adaptated to the ingestion of soil from the deep strata that they use to colonize, while *M. anomala* has a better growth in the upper strata where it is more likely to be found. Therefore, the vertical distribution of the populations does not seem to be a consequence of a present competition for space and food, but rather the result of particular adaptations.

Relative soil ingestion appears to be regulated according to the soil depth ; it decreases with depth as far as it concernes *M. anomala* and increases for the two other species. The mechanisms of this apparent regulation do not seem to be simple.

On the other hand, growth rate and growth efficiency (of which the ratio $\frac{\Delta W\%/day}{\overline{C}/\overline{W}}$ gives an idea), are never proportional to the organic matter content of the soil that decreases regularly with depth. It is therefore to be expected that it is the quality of organic matter and/or the microbial activity of the soil that determines its digestibility by earthworms. Experiments have been designed to test these two last hypotheses with young *M.anomala*.

VARIATIONS OF SOIL INGESTION AND GROWTH RATES OF IMMATURE *M. ANOMALA* BRED IN SOIL ENRICHED WITH DIFFERENT VEGETAL COMPOSTS

Global data from Table 6 are too coarse to explain the results described in the previous paragraph. However, this organic matter seems to be much too diluted to allow more precise chemical analysis. In order to overcome this difficulty, we have added to a control soil (from the stratum 10-25 cm of a shrub savanna) diverse vegetal compost which is easier to analyze.

Methods

Compost was made of pulverised roots or leaves of the graminea *Loudetia simplex* decomposed in aerobic or anaerobic conditions during 0, 2, 5 or 10 weeks. Fifteen series of cultures were undertaken : one control was whithout compost and fourteen were enriched with 1% of each of the prepared powders. Each series was composed of two cultures of five young *M. anomala*. The experiment lasted 10 weeks so that the total lenght of each series was 700 worms x days.

Results

In all of the series, the growth rate was higher than in the control. The grass aerobic composts gave the best results, but the other series give similar figures with smaller amplitudes (Table 8).

Mean growth efficiency (E = $\frac{10^3\ \Delta W\%/day}{\overline{C}/\overline{W}}$) is 107 in the control, 150 in the aerobic root, 155 in the anaerobic root, 236 in the anaerobic leaf and 355 in the aerobic leaf composts.

One percent of leaf powder added to control soil permits the doubling of mean daily growth rate that raises from 1.93% to 4.14% (Fig. 5). The best growth is observed with the two weeks earobic compost (LA_2) : 4.26%. Then it decreases with more decomposed substrata : 3.86% with LA_5 and 2.31% with LA_{10}. The soil ingestion curve is exactly opposite. Ingestion is maximum in the control soil ($\overline{C}/\overline{W}$ = 18g dry soil/g fresh weight), decreasing with leaf powder L_0 (10.7), and is minimum with compost LA_2 (7.7). It increases with LA_5 (12.2) and LA_{10} (12.4), remaining, however, inferior to control value.

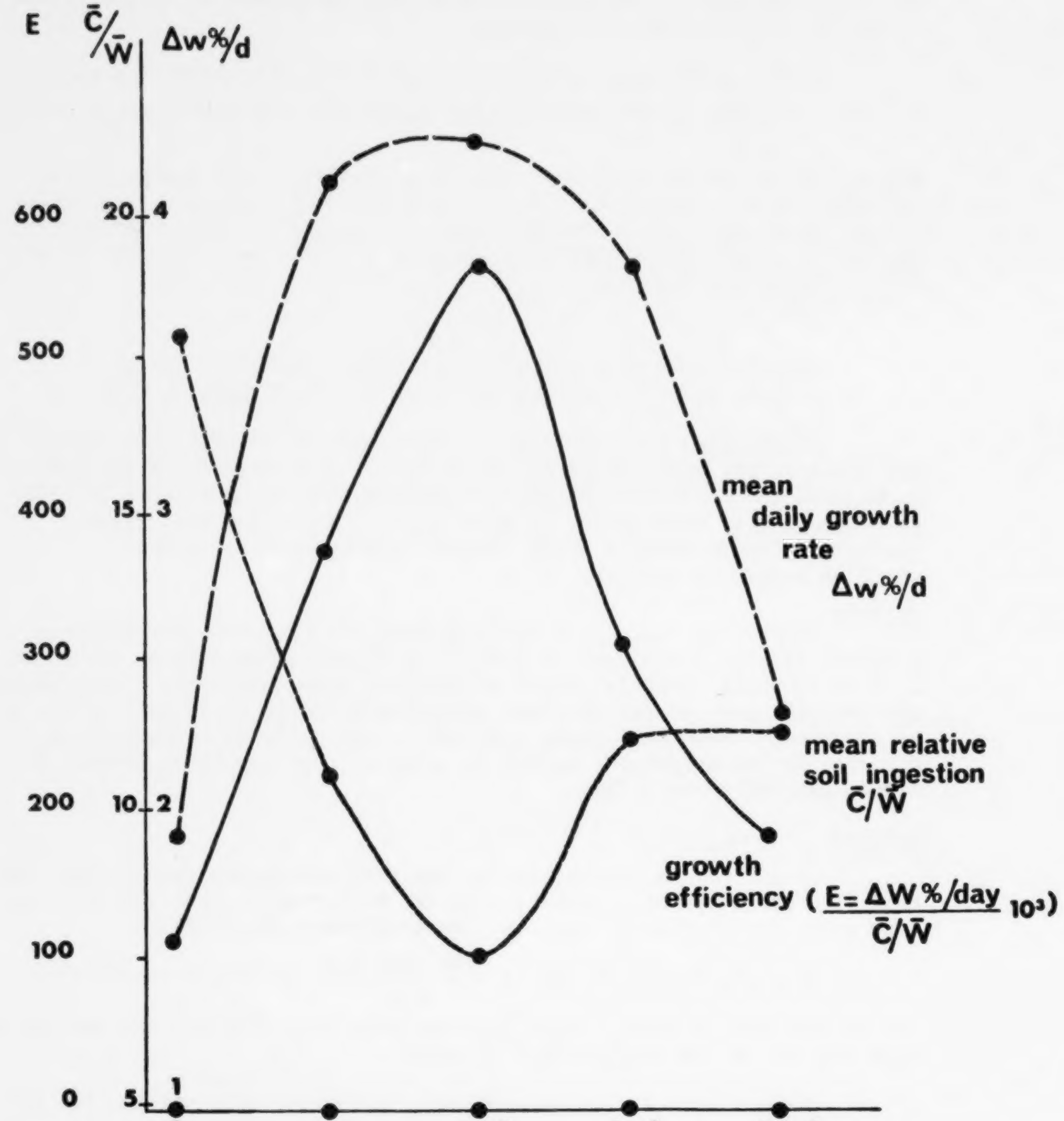


FIGURE 5. Mean growth rates, relative ingestion and growth efficiency of young *M. anomala* fed with soil from the 10-25 cm layer of a shrub savanna (C) enriched with different pulverized grassleaf aerobic composts (L_0 : grassleaf, LA_2 : two weeks aerobic compost, LA_5 : five weeks...).

TABLE 8. Global results of young *M. anomala* cultures in control soil (T) enriched with different vegetal composts (L : leaf, R : roots ; A : aerobic, N : anaerobic ; 2, 5, 10 : time of decomposition). ΔW %/day : mean daily growth rate ; $\overline{C}/\overline{W}$: mean relative soil ingestion ; $E = 10^3 \dfrac{\Delta W \ \%/\text{day}}{\overline{C}/\overline{W}}$ ⇒ growth efficiency rate.

		Serie	ΔW %/d	$\overline{C}/\overline{W}$	E
		T	1.93	18.0	107
Leaf	Aerobic	L_0	4.14	10.7	368
		LA_2	4.26	7.6	564
		LA_5	3.86	12.2	316
		LA_{10}	2.31	12.4	186
	Anaerobic	LN_2	3.60	10.5	338
		LN_5	3.39	15.0	226
		LN_{10}	1.99	13.7	145
Roots	Aerobic	R_0	2.33	13.0	210
		RA_2	3.06	14.4	213
		RA_5	2.73	20.2	135
		RA_{10}	1.45	14.4	101
	Anaerobic	RN_2	2.75	15.5	178
		RN_5	2.77	18.6	149
		RN_{10}	2.03	14.6	139

The growth efficiency rate (E) is minimal in the control (E = 107), reaching 261 with L_0, and culminating with LA_2 (457). It then diminishes in more humified composts : 316 with LA_5 and 186 with LA_{10}.

Consequently, the growth of young *M. anomala* is not proportional to the organic matter content of the ingested soil, but it seems to be closely dependent on its composition. On the other hand, the quantity of ingested soil shows great variations : when the medium is highly nutritive, it can decrease, reaching less than 50% of control value.

We have tried to find a relationship between the composition of the added powders and the culture data. With this purpose, the energetic value of the different glucidic fractions (hydrosoluble fractions extracted before and after lipid extraction and hemicellulosis) have been evaluated by measuring their reducing power. The separation of these different constituents has been made according to methods described by JARRIGE (1961), and the reduction potential measured by the HAGEDORN and JENSEN micromethod. Lipid content has also been measured.

The progressive humification of grassleaf powder is followed by a clear decrease of the energetic value of hydrosoluble fractions and lipids, whereas hemicellulosis increases (Table 9). All things considered, the addition of 1% of these powders do not even double, in the best case, the global nutritive value of the ingested soil. On the other hand, the variations observed show a regular decrease of the soluble energetic fraction while the less digestible hemicellulosis increases.

TABLE 9. Energetic values of the different glucidic fractions (in mg equivalent glucose per g) and lipid content (in mg/g) of the grass-leaf aerobic composts and control soil.

	Hydrosoluble fraction 1	Lipids	Hydrosoluble fraction 2	Hemicellulosis
T	0.35	< 0.05	ε	2.1
L_0	24.7	6.3	2.9	13.3
LA_2	9.0	4.6	2.3	14.0
LA_5	7.4	3.6	1.4	15.0
LA_{10}	6.9	3.4	1.0	16.1

These results do not explain the variations of growth rate and especially of growth efficiency that culminate in the cultures enriched with compost LA_2 (two weeks of aerobic decomposition).

This means that more precise analyses should be performed in order to identify the exact composition of the energetic fraction we measured. An other hypothesis could be that these relations are explained by earthworm-microorganism interrelations, as it is usually mentioned that humivorous animals could feed on microorganisms. In order to test this hypothesis, we have performed some experiments.

PRELIMINARY STUDY OF MICROORGANISM-EARTHWORM INTERRELATIONS

First, we have tried to ascertain if a relation could be established between microbial activity of the ingested soil and earthworm growth. If demonstrated, it could indicate that the earthworm feeds on microorganims or utilizes the product of their metabolism.

Thus we have measured respiration of soils during one week (that is the interval between two changes of the soil in culture). The method used is a macrorespirometric one (Stoklasa) ; CO_2 is extracted by depression and titrated by a system of Barium hydroxyde-oxalic acid (RASHID and SCHAEFER , 1978). The analyzed substratum is pulverized while dry, then moistened and homogenized by repeated stirring, so that the measured respiration is accurate and repeatable. Figure 6_A illustrates the experimental data.

Respiration rate is lowest in the control soil, highest in the soil enriched with 1% undecomposed grassleaf, and it decreases progressively with the gradual humification of grassleaf powder. It remains, however, superior to the control value. The microbial activity seems to be highly stimulated by a substratum rich in easily assimilated energetic elements (the grassleaf), and it decreases progressively when the grassleaf gets more humified ant the soluble fraction less important.

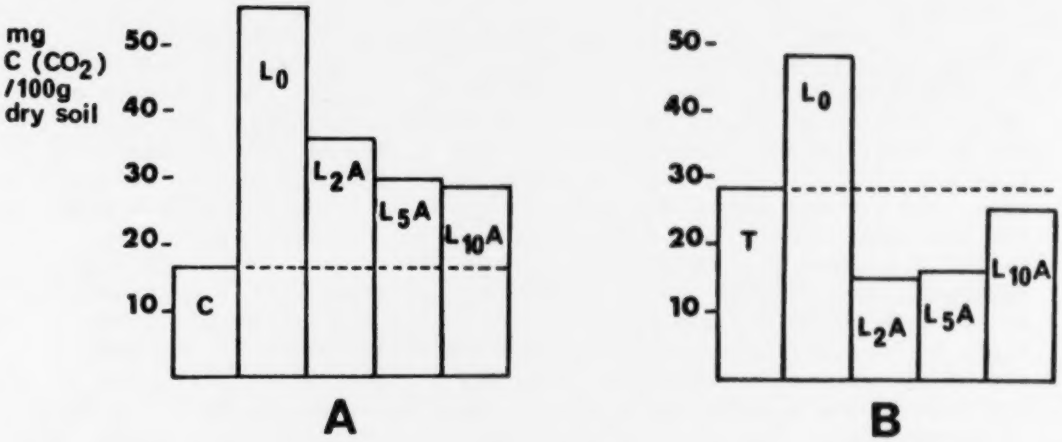


FIGURE 6. Weekly respiration of control soil (C) enriched with 1 % of the different grassleaf aerobic composts (A) and same experiment (B) after replacing control soil by casts of young *M. anomala* (T) fed with the control soil.

The same experiment has been done after having replaced the control soil by the casts of young *M. anomala* fed on this soil. The casts respire much more than the control as the microbial activity is almost doubled (16 to 29 mg. C (CO_2)/100 g dry soil). It is likely that mucus produced by earthworms has a stimulating effect ; the mechanical action produced by earthworms is also responsible for this stimulation as it induces movement of substrata and a modification of microorganism associations. In return, addition of grassleaf and composts powders to the casts gives respiration patterns inferior to the previous ones. With grassleaf (L_0) the decrease is low (55 to 47 mg. C (CO_2)/100 g dry soil). It is, however, most important with two-weeks-old leaf compost (LA_2) (35 to 15) which gives the lowest respiration rate, and more humified composts LA_5 (29 to 16) and LA_{10} (28 to 26), whose respiration is still inferior to the cast.

It seems, therefore, that an explanation to the *M. anomala* growth variations could be derived from these results. The earthworm could produce in its casts a substance that inhibits the activity of microorganisms in lightly humified substrata. This inhibition would not be apparant with added grassleaf powder. Its soluble energetic fraction is important enough to avoid competition between microorganisms and the earthworm. The inhibitory effect could be maximum with the two weeks compost and diminishes with more humified substrata. It would reverse in control soil because the organic matter is highly humified. Such results can be expected if we suppose that earthworms do not feed on soil microorganisms but rather can in certain conditions be in competition with them for the exploitation of the most digestible energetic substrata. When given a riche food (L_0), the inhibition is low because there is no competition. With a more humified substratum less rich in soluble energetic substances (LA_2), competition becomes maximal. The effect is reversed when the humification process is more advanced ; competition turns to symbiosis as earthworms try to utilize energetic substances produced by microorganisms from more complex substrata (hemicellulosis, cellulosis) that they cannot alone digest. In the control soil poor in hydrosoluble elements, the microbial activity is then clearly favoured.

CONCLUSIONS

These preliminary results indicate that geophagous earthworm nutrition from soil organic matter depends on many complex factors. It is clear that abundance of organic matter and, above all, its composition play an important role ; nevertheless it is perhaps more understanding the interactions of each species with the soil microflora that will explain the particular adaptation which make possible the wide functional diversity of the geophagous community.

ACKNOWLEDGEMENTS

We are greatly indebted to Roger VUATTOUX Director of the Lamto Ecological Research Station for his help in the resolution of many material problems and to Spyros MOLFETAS and Donald SCHWERT for the revision of the text.

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QUESTIONS and COMMENTS

C. ANDERSEN: Was there any difference in soil consumption between the investigated species?

Was there any difference in the gut anatomy of the superficial living species contrary to the deep living species?

P. LAVELLE: These differences are discussed in the text.

The gross anatomy as studied for systematic purposes did not show differences in the shape and size of typhlosoles. It was although demonstrated that the deep dwelling species are relatively longer than "surface" dwelling and have a longer gut (LAVELLE, 1973. Peuplements et production des vers de terre dans les savanes de Lamto [Cote d'Ivoire] Ann. Univ. Abidjan, E, VI [2] : 79-98.

S.B. HILL: I think that successional changes in microflora should be taken into account before concluding that earthworms are not deriving nutrients directly or indirectly from decomposer microorganisms. Your results could simply mean that the "initial" and "late" stage microflora in the succession are less attractive to earthworms than those in the "mid" stage.

P. LAVELLE: These earthworms eat the soil as it is, so it is impossible for them to select certain microorganisms for their feeding. We also think that the microorganisms that develop in the early stages of decomposition feed mostly on simple and very digestible substrates. So the products of their metabolism are expected to be more complex and thus less digestible for the worm.

G. BENGTSSON: You evidently have difficulties proving any positive correlation between growth rate of the animals and the concentration of less digestible organic compounds in the soils. Why did you make these analyses in preference for analyses on more digestible compounds such as amino acids, simple carbohydrates and fatty acids and on the enzymatic activity, which should represent part of the microbial activity.

P. LAVELLE: I have in fact measured these digestible compounds as I think that simple carbohydrates, amino and fatty acids are contained in the two hydrosoluble fractions we extracted. As far as microbial activity is concerned we preferred, in this preliminary study, making total respiration measures that are easier to realize.

C. KNÄPPER: Die aufgeworfenen Fragen sind sehr sinnvoll. Wir bestätigen die Angaben und können behaupten, dass in unserer Arbeit in Rio Grande do Sul einige Arten der Gattung Pheretima zur Oberfläche kommen wenn ihre "nicho" mit Stroh bedecht sind.

DEVELOPMENT AND FECUNDITY OF THE MANURE WORM, *Eisenia foetida* (Annelida: Lumbricidae), UNDER LABORATORY CONDITIONS

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INTRODUCTION

The lay and technical literature are replete with conflicting claims on the growth rates and fecundity of the manure worm, Eisenia foetida (Savigny, 1826) and even its identity (Fosgate and Babb, 1972). In addition, suspected fraudulent claims were and continue to be made by dishonest worm breeders seeking to entice more people into the manure worm breeding business. We undertook this research project to provide some clear answers as to what the growth rates and fecundity of the manure worm are under a variety of temperature and worm density conditions.

METHODS AND MATERIALS

Several hundred specimens of the manure worm were obtained from an Ontario grower, verified by key (Reynolds, 1977) as E. foetida; and used as a continuously reared laboratory culture.

Experiments were carried out on worms confined to plastic petri dishes (15 cm dia. X 2 cm deep with a 15 cm dia. while filter paper on the bottom) containing approximately 130 ml of moist (82% water by weight) manure (leached dairy cattle manure:maple sawdust, 3:1 or leached horse manure) pH of both approx. 6.8, weighing about 100 gm; the manure was replaced weekly. Temperature dependent experiments were performed in controlled environment cabinets with ±1C° precision. Dishes were checked daily to remove cocoons which were placed singly in 4 dram clear plastic snap cap vials which contained a moist filter paper disc. When the young worms hatched from the cocoons, the date was marked on the vial label and their subsequent growth and development noted.

RESULTS

The length of one life cycle varied from a mean of 51.5 days at 25°C to more than 166 days at 13°C, from freshly deposited cocoon through clitellate worm and deposition of the next generation of cocoons

(Table 1).

TABLE 1: Maturation periods for *Eisenia foetida* at various temperatures on dairy cattle manure.

	Elapsed time (days) for maturity periods				
Temp.°C	To Hatch	To Incipient Clitellum	To Complete Clitellum	To Cocoon Production	No. Worms Studied
13	45.2	107.5	116.9	none by 166	22
16	31.2	68.8	77.3	98.6	25
19	26.7	58.7	62.2	70.3	24
22	19.8	46.0	53.5	55.5	11
25	18.9	45.1	48.1	51.5	16

The number of young worms hatching from viable or fertile cocoons incubated at 25°C varied from 1 to 11 (one event) with a mean of 3.35±0.28 of 310 cocoons studied. The percentage hatch of cocoons obtained on horse manure at 25°C varied from 50.9 to 90 with a mean of 80.7 (Table 2).

TABLE 2: Percentage hatch of *Eisenia foetida* cocoons in horse manure at 25°C.

Dish No.	No. of cocoons	Mean No. Worms/Cocoon	% Hatch
1	39	2.80	89.7
2	53	3.81	83.0
3	53	2.75	50.9
4	22	3.14	86.4
5	38	3.55	89.5
6	33	4.24	87.9
7	32	1.45	50.0
8	40	4.70	90.0
Total	310	Grand mean	80.7

Increasing temperature reduces both the percentage hatch of cocoons from 57.3% and 60.8% at 13°C and 16°C to 41.2% at 25°C, and the number of young worms produced per cocoon (Table 3).

As the density of mature clitellate worms per unit volume of manure increases the number of cocoons/parent/wk, the hatching fraction, and the number of young worms/cocoon declines. If these 3 numbers are multiplied

TABLE 3. Effect of temperature on the no. of worms produced per cocoon and the percentage hatch of Eisenia foetida cocoons (Dairy Cattle Manure).

Temp. °C	Mean No. Young worms/ cocoon	Mean No. Young Worms/ Viable Cocoon	Total No. Cocoons	No. Viable Cocoons	% Hatch
13	1.71	2.97[a]	82	47	57.3
16	1.94	3.23[a]	78	48	60.3
19	1.80	2.90[a]	73	39	53.0
22	1.01	2.13[b]	80	38	47.5
25	0.65	1.58[b]	80	33	41.2

a, b - Numbers followed by the same letter are not significantly different from one another. Numbers followed by different letters are significantly different from each other ($P<0.05$) Duncan's New Multiple Range Test.

together for each density level (Table 4), we obtain a "productivity" figure expressed as No. of young worms/parent worm/wk which varies from 5.45 at the lowest parent density to 1.19 at the highest.

TABLE 4. Effect of parent crowding (density) on young worm production at 25°C on dairy cattle manure (200 ml/dish) over 14 weeks.

No. Parent Worms/Dish	No. Cocoons Produced/ Parent/wk	Hatching Fraction	No. Young Worms/ Cocoon	No. Young Worms/ Parent/ wk*
2	2.0	.79	3.45	5.45
4	1.2	.73	2.47	2.16
6	0.8	.77	2.56	1.58
8	1.2	.42	2.36	1.19

* Product of Columns 2, 3 and 4.

Population density also had an effect on weight over the 14 week duration of the experiment. At densities above 2 worms per dish, reductions of between 11.1 and 15.6% occurred (Table 5).

TABLE 5. Effect of population density on weight of *Eisenia foetida* at 25°C over 14 weeks (2 replicates for each density).

No. worms/ Dish	Mean Wt (gm) at start	Mean Wt (gm) at 14 wks.	Δ Wt.
2	0.44	0.44	0
4	0.45	0.38	-15.6
6	0.45	0.40	-11.1
8	0.45	0.38	-15.6

DISCUSSION

The rate of development is, as expected, positively correlated with temperature. Obviously growing worms unsheltered, in cold weather climates will result in dramatically reduced production during the winter months. Low temperatures also suppress either mating behaviour or reduce cocoon production; since the clitellate condition is reached at 116.9 days at 13°C, but no cocoons are produced for at least 50 days following.

It is also interesting to note that at 25°C a life cycle can be completed in 51.5 days as opposed to the 60-90 days suggested by Gaddie and Douglas (1975).

The varied hatchability of the cocoons is similar to that found by Watanabe and Tsukamoto (1976). The maximum number of worms they found from one cocoon was seven; herein we report a maximum of 11. Also, in results similar to theirs we noted a range in the mean number of worms produced per cocoon from 3.35 in the autumn to 1.58 in the winter. This is a long way from the mean of seven proposed by Gaddie and Douglas (1975).

From Table 3 it appears that increasing incubation temperatures are negatively correlated to the number of young worms produced per cocoon. There are perhaps a number of possible causes of this result, but there is the possibility that at higher temperatures respiration rates within the cocoon might only be maintained with difficulty and, if there are several worms developing, this could result in cocoon mortality which is reflected in the lower percentage hatch at higher temperatures.

The parent worm density had an unexpected result on the number of worms produced per cocoon. Somehow the reduced density of mature worms results in a larger mean number of worms/cocoon being produced, a higher hatchability percentage (fertility rate), and a larger number of cocoons/parent being produced. Presumably this allows for a more rapid population expansion to ultilize the larger food resource (manure) available at the lower parent worm densities. A similar effect has been observed with the waterflea, Daphnia pulex, where fecundity was reduced at higher densities (Frank, Boll, and Kelly, 1957).

The average number of cocoons/parent/wk varied from 2.0 to 0.8 over 14 weeks during the winter. Graff (1978) averaged from 5.0 to 3.5 on 14 day tests during spring and summer. We don't feel there is a conflict in the results here because we observed many cases where worms produced 5 or more cocoons/week, but this rate would only be maintained for 2 or 3 weeks. Naturally over longer periods this average would decline which has considerable implications for some of the more outrageous claims of growers where high cocoon production rates are assumed to be maintained over long periods.

We have received several reports from commercial worm growers concerning sudden reductions in size (weight) of worms. This was usually attributed to reduced food and/or moisture supply. Since fresh manure was supplied weekly to our cultures, we do not feel that this is necessarily the reason. There is, however, some correlation between worm density and weight loss.

CONCLUSIONS

The lumbricid worm, E. foetida, can complete a life cycle in as few as 51.5 days. Maturation is strongly correlated with temperature in the range 13°C to 25°C. The maximum number of worms found in a single cocoon was 11, but the mean lay between 2 and 3. Parent worm density is negatively correlated to cocoon production, cocoon fertility and the number of young worms produced from a cocoon.

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The authors acknowledge the technical assistance of Ms. P. Vander Deen, and thank Mr. J. L. Lewis of Jimaur Bio-Organic Cultures Ltd. for supplying the worm culture. Contribution No. 764, Research Institute, Agriculture Canada, London.

QUESTIONS and COMMENTS

J.E. SATCHELL: Can you suggest the mechanism causing the weight losses at higher population density?

A.D. TOMLIN: No. We are fairly certain, however, that the weight loss was not due to reduced food substrates since they were replenished weekly.

A.J. REINECKE: Did you consider the possibility that diurnal fluctuation in temperature with a mean of say, 20° C could lead to quite different results than a constant temperature of 20°C as far as time until hatching goes?

A.D. TOMLIN: Yes, but we were interested mainly in finding the minimum time for development from deposition of cocoon to sexual maturity. Introducing another parameter would have complicated the experiments even further.

D. LIVINGSTONE: Were the manures leached of urine?

A.D. TOMLIN: Yes and the average pH was 6.8.

SEASONAL VARIATIONS OF SEX-RATIO IN FOREST GROUND-BEETLES NATURAL POPULATION

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Because of its importance for reproduction, the sex-ratio of a population is one of the factors effectively influencing the dynamic of a population. This ratio varies with the species and population age (DAJOZ, 1971); in Carabid beetles, it is generally thought to have value one (PENNEY, 1967), but seems to vary with the habitat (MOSAKOWSKI, 1970). V.d. DRIFT (1951) observed its variations also with the seasons; a problem about which thereare a very few studies.

It is difficult to know the sex-ratio of a natural population of Carabidae because the traps are not identically effective for both sexes : in fact, GRUM (1962) shows that the females locomotion, more important at the period of laying the eggs, alter the male/female ratio of the captures. This work studies the seasonal variations of the sex-ratio according to the activity cycle of Carabidae.

METHOD & MATERIAL

Animals have been trapped from february 1972 to january 1974 included. The traps are pitfalls of BOUCHE type (1972); the captured animals are killed and fixed with a NaCl saturated solution. A wire-netting stops the leaves from falling in the trap. The 13 pitfall traps are visited each month; captured animals are taken out and kept in alcohol 70°.

Study place : the "Tillaie" biological reserve is an area of 33.74 ha, situated in the N.E. fourth of the "Forêt de Fontainebleau". The 700 m2 under study are a part of an Aspero Fagion established on a mull-moder: the organic matter content is 4-5%, the percentage base saturation 30%; pH is 4.5 (BOUCHON et al. 1976).

All insects were dissected for measuring and weighing the gonads.

RESULTS, DISCUSSION

At "La Tillaie", 12 species of Carabid-beetles belonging to four families were captured : Carabidae, Nebriidae, Trechidae, Pterostichidae. Captures were homogenous between the two years according to the number of captures and to their specific distribution. Thus, we summarized data from both years : we shall then analyse the sex-ratio of both years together.

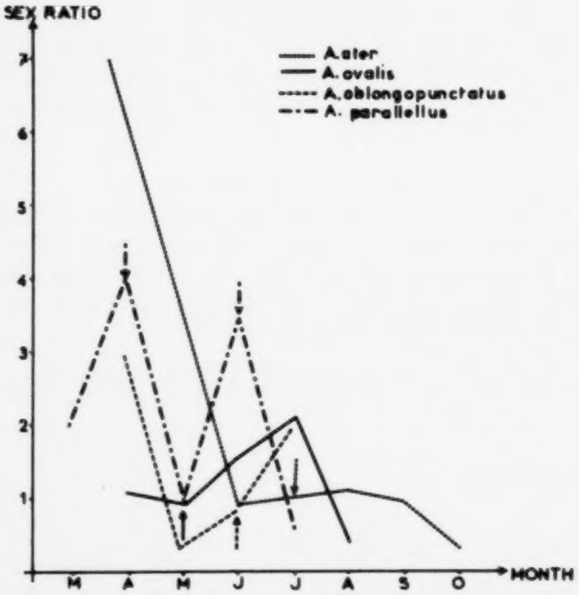
Moreover, we shall be interested here only on some Pterostichidae. There were six species of this family in the traps : Argutor oblongopunctatus, Abax ater, Abax parallellus, Abax ovalis, Synuchus nivalis, Calathus piceus. The former four, three of which belong to the same genus, constitue 87.89% of all the captures. Here, we shall not take in account S. nivalis captured once during 24 months and C. piceus, as we captured two males and 32 females of this species.

We showed (BENEST and CANCELA da FONSECA, 1979) that the activity periods of these animals were :

A. oblogonpunctatus : march-july, with a maximum in june;
A. ater : april-october, with a maximum in july;
A. parallellus : march-september, with maxima in april and june;
A. ovalis : april-august with a maximum in may.

Thus we shall observe the evolution of the sex-ratio (♂/♀) during these periods. The activity periods we observed at "La Tillaie" correspond to the dates of reproduction of these species : spring for A.oblongopunctatus and autumn for A.ater for example.

Generally, observations provide a sex-ratio of value one (PENNEY, l.c.). While in the four populations we studied, this ratio is more often different from one (fig.1). However, we draw attention on the following facts : 1) sex-ratio varies according to the months; 2) on the dates of maximum activity, the sex-ratio is nearly one for A. ater, A. ovalis and A. oblongopunctatus, and 3.5 for A. parallellus.



ARROWS INDICATE ACTIVITY MAXIMUM OF EACH SPECIES

FIGURE 1 : Variations of sex-ratio according to seasons.

Thus, it clearly appears that for the 3 first species the number of males is equal to the number of females at the time of mating and laying eggs; this has already been observed by v.d.DRIFT (l.c.).

However, this is not true for *A.parallellus*, the behavior of which is different from that of the other three species : in fact, this species shows a great excess of males on the two dates of maximum activity. This particular behavior deserves attention for it clearly distinguishes *A. parallellus* from the two other *Abax*.

Thus, it is clear that, for these four species, the share of each sex to the active population varies with time : this phenomena is related to the different activity of each sex according to the season. This hypothese , although disputed by some author (SZYSZKO,1976) is fully corroborated for *A. ater*, *A. ovalis* and *A. oblongopunctatus*. However, it does not fit *A. parallellus*, the behavior of which is particular : the females of this species are the only ones, among the known *Carabidae*, to be able to lay two batches of eggs in one year (LÖSER, 1970).

For a better explanation of these phenomena, we must study the gonadal state of the captured animals. By the males, the most important variations are observed on the accessory glands (CORNIC, 1970). Though JONES (1979) found it difficult to study them on newly captured animals; this is due, in part, to the technic : pitfalls trap active animals from a locomotory point of view as well as from a sexual point of view. Thus we could not observe any significative variations considering either the diameter or the dry weight of the glands. While by the females, it is easy to count and weight the eggs contained in the abdomen. Therefore, the following results concern only the females.

The relation between the locomotory activity period and the reproduction period appears clearly in the four species from the fact that :

1) as soon as the first captures of the year, some female carry eggs, but those of *A. ovalis*;

2) eggs are only produced during the period of important activity (BENEST-CANCELA da FONSECA,l.c.)

3) variations of the proportion of egg-carrying females follow quite closely the locomotory activity variations known from the captures.

FIGURE 2 : Variations of egg production

$\boxed{A}$: Abax ater;

$\boxed{B}$: Abax ovalis;

$\boxed{C}$: Abax parallellus;

$\boxed{D}$: Argutor oblongopunctatus;

① : ——— Ratio (%) : egg-carrying females / all captured females;

……… Total number of eggs;

② : Average number of eggs per females in the population;

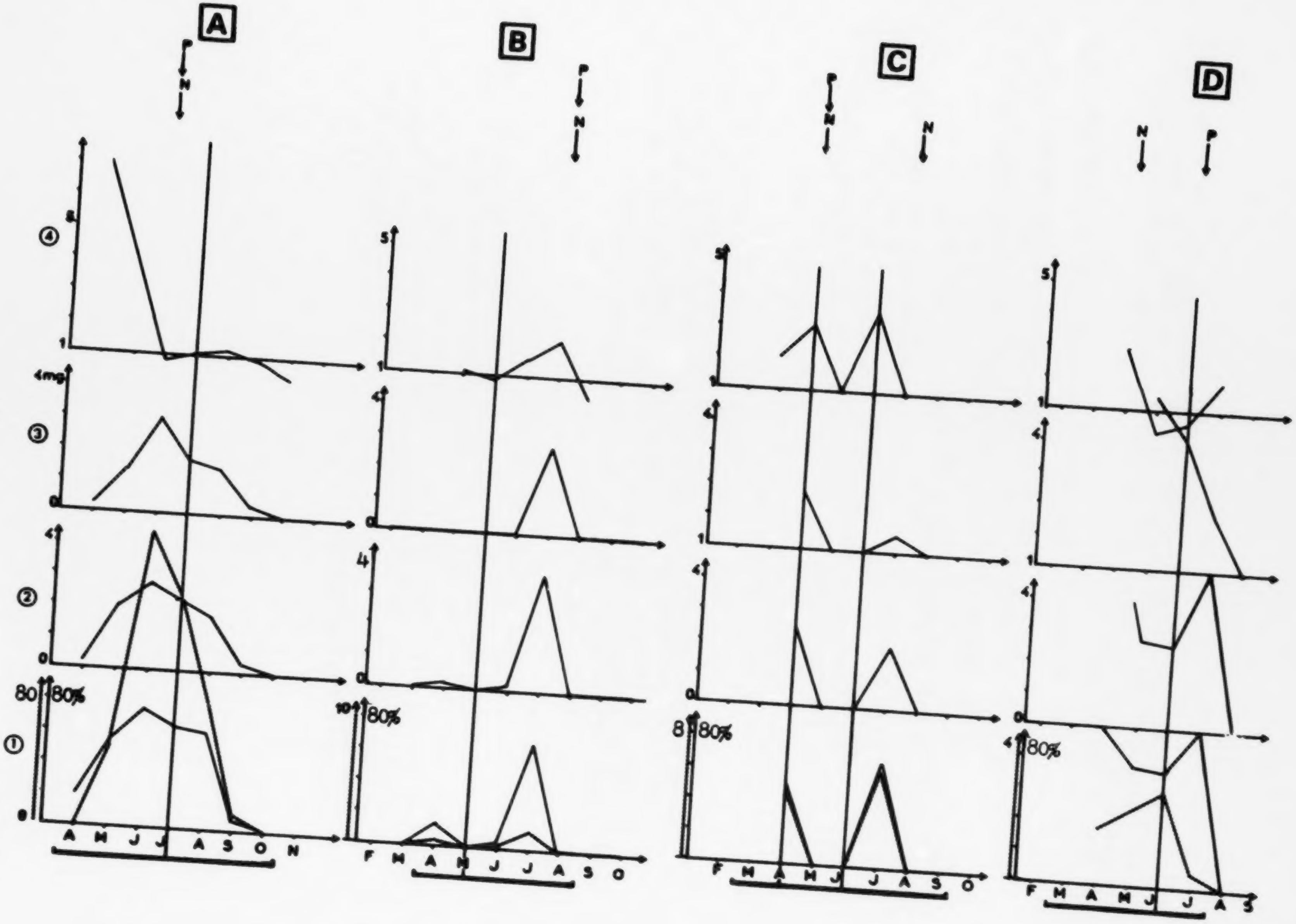
③ : Average weight of eggs per females in the population;

④ : Variation of the sex-ratio;

$\overset{P}{\downarrow}$: Date if maximum weight of one single egg;

$\overset{N}{\downarrow}$: Date of maximum number of eggs carried by one female.

Figure 2: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On the contrary, the production of eggs is not at a maximum when the activity is maximum i. e. when the sex-ratio (♂/♀) is of value one. We measured egg-production with four criteria (fig.2) :

- the number of eggs per female in the population;
- the maximum number of eggs carried by one female;
- the egg weight per female in the population;
- the maximum weight of a single egg.

These four criteria provide very homogenous data for the three Abax : by the three species, they are maximum at the time when each population contains the most egg-carrying females. This is not true for A. oblongopunctatus; however, we must recall that for this species only one female was caught in april and in july, and it carried eggs : this constitues a bias in the data.

By A. ater, the time of the maximum egg production is one month earlier than the time of maximum activity; for A. ovalis, maximum egg production is two months later than maximum activity; for A. parallellus, every maxima happen together in april, but with one month inbetween during summer. There again appears A. parallellus originality.

CONCLUSION

Thus, there appear no relation between egg-production and sex-ratio. In fact, the relation is closer between the period of reproduction and the period of locomotory activity. Reproduction processes consist, among others, of mating and laying eggs : these two processes imply female locomotion first for mating, second for choosing the suitable laying place.

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QUESTIONS and COMMENTS

A. CARTER: Data from pitfall trapping cannot be used alone to determine the actual sex ratio or proportion of teneral to older adults in carabid populations. What comments do you have on this?

G. BENEST: Pitfalls are known to trap only active animals, males or females,teneral or older; in fact, this technique does not give a good estimation of the total population. I only say that the contribution to the active part of the population is different for the males and the females according to the season.

J.A. ADDISON: Do the micromorphological characteristics that you used to discriminate between the two Lithobius species remain constant for all stages in the life cycles of these two species?

G. BENEST: Probably Lithobius sp. do not change micromorphological features according to developmental stages.

But that is not true of all animals. Great differences exist between larvae and imaginals in Coleoptera for example.

A.J. SZUJECKI: Sex ratio in the Carabidae population is not stable, it varies in time and space in relation to the change in environment and in the population. We observed however that sex ratio in the population of Pterostichus oblongopunctatus is rather stable (on the average) in this same site conditions (higher in pure pine stands and lower in rich broadleaf forest). It also changes during the development process in the stands (in various age classes of stands). This may be followed by various degrees of competition between species in the Carabidae community in various site conditions.

H. PETERSEN: Do you have evidence whether the sex-ratio is determined from the egg stage, or is it a consequence of differential mortality between males and females?

Did your experiments with marked animals show different life times for adult males and females?

G. BENEST: Actually there cannot be any answer to the question because pitfalls are concerned only with imagines. Moreover, research on reproduction in Carabid beetles has only begun and very little is known about egg production in natural conditions.

There seem to be no great differences between male and female life times.

P. LAVELLE: How many species is it necessary to study to be able to determine the whole Carabid diet?

G. BENEST: Oligophagous Carabids are rare. Skuravy has demonstrated that some Pterostichidae could eat up to 18 different families of prey. Among these Pterostichidae, Harpalus aeneus eat 14 of these families; moreover it is able to eat eggs and dead animals.

That is the difficulty of this type of work. Carabidae have a very broad spectrum of prey.

INTRODUCTIONS EN SURPOPULATION ET MIGRATIONS DE LOMBRICIENS MARQUÉS

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INTRODUCTION

L'étude écologique fonctionnelle des lombriciens doit, pour l'essentiel, se faire in situ, les données de laboratoire n'offrant présentement aucune garantie, notamment en raison du fait que l'on ne peut que rarement les recouper par des informations acquises en conditions naturelles.

A l'exception de l'étude de certains phénomènes se produisant à la surface du sol, nous sommes obligés généralement de faire des observations destructurant le sol. Ces observations, par prélèvements ou lecture directe dans le sol, nous oblige donc au choix d'emplacements différents à chaque fois. Les informations sont acquises à un instant ; leur répétition permet de constater une série d'images successives se rapportant à des emplacements différents sur des animaux différents de sorte que leur interprétation en terme dynamique est pratiquement impossible dans la plupart des cas (voir cependant Lavelle, 1971, pour des données démographiques). Toutefois, le marquage des animaux permet de retrouver les mêmes cohortes d'individus, voire les mêmes individus, et ainsi de suivre des variations d'états diachroniques (= en fonction du temps).

Distinguons immédiatement les marquages individuels des marquages isotopiques. L'usage d'isotope permet de suivre à l'intérieur d'un organisme, ou en général d'un système, le devenir de cet isotope et ses associations avec des molécules, des tissus, des individus, voire des chaînes trophiques.

Le marquage individuel vise à reconnaître un individu, ou une collection d'individus (= une cohorte), parmi un ensemble plus vaste. De très nombreuses techniques sont théoriquement applicables pour reconnaître ces animaux marqués mais en pratique seules quelques-unes peuvent être efficacement mises en oeuvre. Dans certaines circonstances, les isotopes permettent la reconnaissance d'individus mais généralement cette possibilité est très limitée car les isotopes peu ou faiblement radio-actifs ne se "voient" pas et nécessitent des moyens d'analyse lourds et destructeurs (broyat des tissus) ; quant aux isotopes fortement radio-actifs, ils sont interdits dans la nature. Nous nous sommes donc tournés vers le marquage individuel directement visible (Mazaud, 1979) et non isotopique. Deux approches ont été tentées : la cautérisation individuelle de soies et le marquage coloré.

La cautérisation des soies, d'usage délicat, a des conséquences peu standardisables. Elle pourrait convenir en certains cas au marquage de quelques individus mais ne permet pas de travailler sur des cohortes importantes. Afin de suivre au terrain le devenir de cohortes d'individus, les techniques de coloration ont été éprouvées et étendues. Comme la cautérisation, cette technique est originale à l'exception de l'usage du vert menthe E (VME) proposé antérieurement par U. Meinhardt (1976). Pour apprécier les difficultés pratiques de mise en oeuvre de cette nouvelle méthode, divers lâchers de lombriciens, en surnombre, ont été effectués sur un sol non perturbé préalablement. Puis les lombriciens, marqués ou non, ont été recapturés au lieu de lâchage et autour de ce lieu, ce qui a permis d'acquérir des informations relatives à la migration et à l'effet de surpopulation.

MATERIEL ET METHODE

Marquage des animaux

La technique résulte de multiples essais préalables et de contrôles de l'état physiologique des animaux qui n'ont pas permis de mettre en évidence des troubles profonds chez les lombriciens colorés au laboratoire (Mazaud, 1979). La méthode standard utilisée au terrain comporte les étapes suivantes :

- capture des animaux à la méthode au formol, à proximité du futur lieu de relâcher,
- rinçage,
- pesée,
- détermination en espèces et stades, voire de poids des animaux choisis,
- coloration,
- relâcher dans l'aire d'accueil,
- après un délai variable, recapture dans l'aire et à proximité, des colorés et non colorés.

La coloration des animaux s'effectue par lavage (quelques dizaines de secondes), égouttage-séchage sur grillage plastique (environ 5 minutes), coloration (de 2 mn 30 à 3 mn) par trempage dans une solution colorante, égouttage (quelques secondes) et séchage (3 à 10 mn selon la taille et les espèces). Vingt et un colorants "histologiques" ou "alimentaires" ont été testés ; deux colorants histologiques (rouges) ont donné des résultats encourageants (la safranine et la phloxine) quoique leur toxicité variât avec l'origine des produits. Deux colorants alimentaires le vert menthe E (E 102 + E 132) et la coccine (E 124) rouge ont donné satisfaction : ils furent utilisés au terrain. Deux dispositifs expérimentaux ont été mis en place au terrain, chacun dans une localité différente (Grignon et Cîteaux).

Les essais effectués à Grignon (département des Yvelines) ont été faits en prairie permanente à sol alluvial limono-sableux. Les animaux furent capturés "au formol", colorés en vert (VME) ou rouge (surtout safranine et coccine) pour caractériser dans chaque espèce (*Nicodrilus giardi giardi* (Ribaucourt, 1901) ; *Lumbricus terrestris* L. 1758 em. Sims, 1956 ; *Allolobophora icterica icterica* (Savigny, 1826)) des classes de poids, relâchés dans une petite aire de 0,1 m^2 environ différente du lieu de capture, recapturés, selon trois zones concentriques (fig. 1) l'aire centrale PM recouvrant l'aire de relâcher. Les emplacements de lâcher étaient distants de 7 m les uns des autres. Les dates des lâchers et la durée du séjour au terrain ont été fort variables.

L'expérience de Cîteaux (département de la Côte d'Or) a été faite sur la prairie servant à la majorité des études fonctionnelles de lombriciens (P. 433). C'est une prairie permanente à sol limono-argileux à pseudogley. Les animaux capturés au formol furent colorés au VME après identification en espèces et stades (*Nicodrilus nocturnus* (Evans, 1946) ; *N. longus longus* (Ude, 1886) ; *N. longus ripicola* Bouché, 1972 parmi les anéciques ; *Lumbricus castaneus* (Savigny, 1826) épigé ; enfin, pour les endogés, *N. caliginosus caliginosus* (Savigny, 1826) ; *Allolobophora icterica icterica* (Savigny, 1826) et *A. rosea rosea* (Savigny, 1826)). Au relâcher, les animaux furent ré-introduits en 165 points en vidant 165 boîtes ayant reçu 5 662 individus marqués. Toutes ces boîtes ont reçu uniformément les anéciques mais, faute d'un nombre suffisant d'animaux, seulement la moitié d'entre elles ont reçu les autres animaux. D'où deux zones différentes dans l'aire de lâcher en raison des peuplements introduits, ceux-ci ayant une nature différente (catégorie écologique) et un niveau différent : surcharge moyenne 17 % mais 22 % dans la zone à faune totale (Zt) et 13 % dans la zone à allochtones exclusivement anéciques (Za) (pourcentages établis par rapport à un peuplement autochtone de 200 individus/m^2) (voir fig. 2).

Les prélèvements ont été effectués avec la méthode formol-bêche. Chaque mois, 4 bandes de 5 m x 1 m ont été échantillonnées à cheval sur l'aire de lâcher et l'extérieur (2 m à l'intérieur et 3 m à l'extérieur) de façon à recenser d'éventuels migrants hors de l'aire. La disposition des prélevats est donnée fig. 3 et la chronologie tableau 1. Les prélevats quantitatifs sont appelés A, B, C, D, E à partir de l'axe médian de l'aire, ils sont dits qualitatifs si l'on y ajoute les animaux récoltés au même niveau par rapport à l'axe médian, hors du m^2 délimité pour la recapture. Les bandes des prélèvements n'ont pas toutes été utilisées en raison d'une saison automnale 1978 extrêmement sèche.

RESULTATS

Lâchers ponctuels répétés : Grignon

A Grignon, on observe une baisse de captures des animaux marqués et non marqués en fonction du temps (tableau 2). Si l'on admet que les résidus du modèle linéaire utilisé sont des variables aléatoires normales non corrélées et de même variance (ce que nous n'avons pu vérifier), les coefficients du modèle sont significativement différents de zéro au seuil 1 %. Ceci permet de préciser le devenir des animaux marqués après le lâcher : 40 % sont recapturables "au formol", 10 % perdent leur coloration. Les 50 % restant sont non extraits du sol ou disparus par mortalité et migration. La diminution dans le temps (évolution chronologique) du nombre de vers marqués et recapturés traduit à la fois un dépeuplement mais aussi souvent l'influence de la sécheresse et 1,7 % de perte de colo-

FIGURE 1 : Les aires des trois prélevats de recaptures effectués à chaque point de lâcher à Grignon.

FIGURE 1

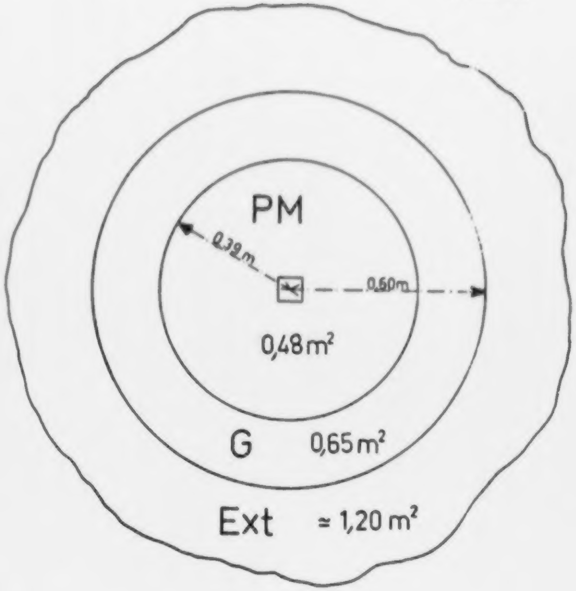

PM
0,39 m
0,60 m
0,48 m²
G
0,65 m²
Ext
≃ 1,20 m²

FIGURE 2

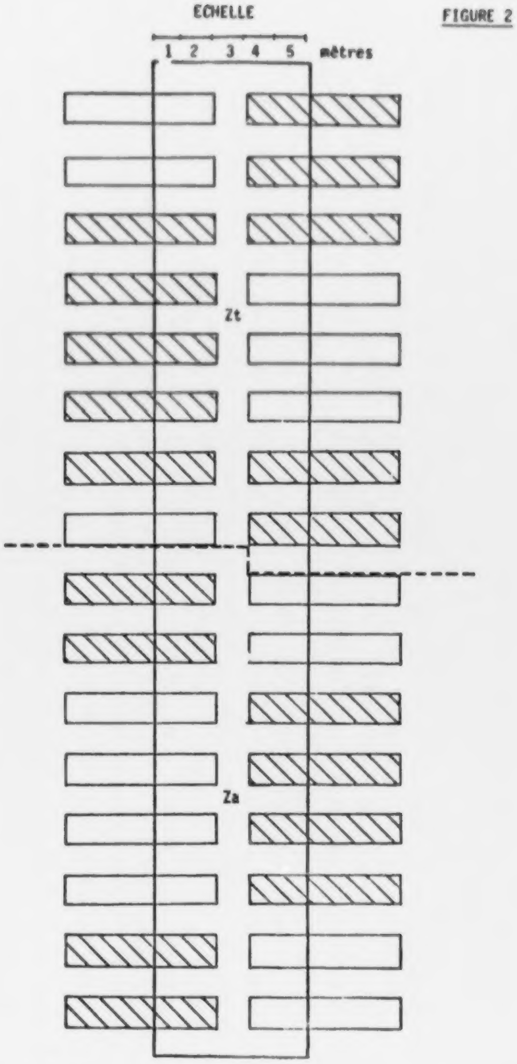

ECHELLE
1 2 3 4 5 mètres
Zt
Za

FIGURE 2 : L'aire de lâcher (aires Zt et Za) et les bandes de prélèvements pour recapture (les bandes hachurées ont été effectivement prélevées).

ration par mois ; ces phénomènes ne peuvent être malheureusement distingués.

TABLEAU 1

Cîteaux. Conditions et chronologie des recaptures. T : température du sol à 10 cm de profondeur et température moyenne mensuelle de l'air (abbaye de Cîteaux). pF du sol à 10 cm de profondeur. D : durée de séjour sur le terrain des animaux recapturés (en jours).

N°	Date		T		pF	D
			sol	air		
		Décembre 77		3		
01	11	Janvier 78	2	1	2,4	46
11	13		2		2,4	48
21	30		4			63
31	31		4		2,4	64
02	27	Février	7	2	2,3	91
12	28		7		2,6	92
22	13	Mars	10	7	2,8	105
32	14		7		2,1	106
03	28		10		2,1	120
13	29		10		2,2	121
23	11	Avril	10	7	2,6	134
33	12		8		2,8	135
04	25		12		2,3	148
14			12		2,3	
24	22	Mai	14	12	2,6	175
34	23		13		2,5	176
05	6	Juin	21	15	3,0	190
15			21		3,0	

TABLEAU 2

Evolution dans le temps des recaptures de vers marqués et des captures globales. Régressions linéaires : $y = ax + b$. I.C. : intervalles de confiance des coefficients a et b.

y	% de marqués recapturés par rapport aux lâchés	nombre total de vers capturés (colorés ou non)
x	durée de séjour	évolution chronologique
équation	$y = -0,146\ x + 40,3$	$y = -0,659\ x + 388$
I.C. (seuil 0,01)	$-0,246 < a < -0,046$ $25,8 < b < 54,7$	$-1,237 < a < -0,081$ $264 < b < 512$

FIGURE 3

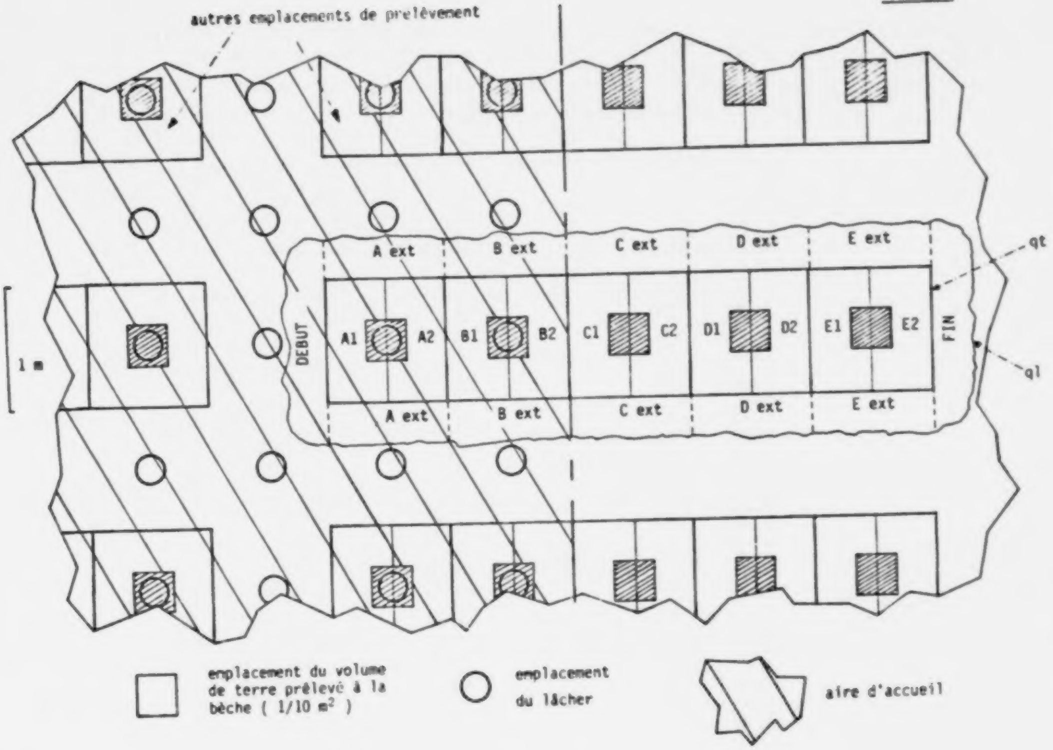

autres emplacements de prelèvement
A ext
B ext
C ext
D ext
E ext
qt
DEBUT
A1
A2
B1
B2
C1
C2
D1
D2
E1
E2
FIN
ql
1 m
A ext
B ext
C ext
D ext
E ext
emplacement du volume de terre prélevé à la bêche (1/10 m²)
emplacement du lâcher
aire d'accueil

FIGURE 3 : Division d'une bande de prélèvement en prélevats. Dix prélevats formol quantitatifs de 0,5 m^2, cinq prélevats quantitatifs bêche après formol de 0,1 m^2 et sept prélevats externes qualitatifs au formol.

Globalement, la migration s'observe sur 258 animaux recapturés dont 69 seulement l'ont été hors de la surface centrale PM (fig. 4) : pour un séjour moyen de 3 mois et demi, seulement 27 % des marqués ont migré hors de l'aire centrale. La migration est donc faible et celle hors de l'aire d'expérience (environ 2,3 m^2) a donc dû être réduite.

Le résultat en fonction du temps (tableau 3) permet de mettre en évidence une émigration progressive des animaux marqués (tableau 4). Dans les surfaces G et Ext, le nombre de recapturés croît dans le temps (en moyenne par jour) de 0,12 % des animaux lâchés. La pente de la droite de régression est différente de 0 au seuil 5 % (équation : $y = 0,123\ x + 0,994$ $y = \%$; x = durée en jours). Cette augmentation se fait malgré une surface de recapture peut-être trop petite, les insuffisances de la méthode au formol et la mortalité avec le temps.

TABLEAU 3

Grignon. Evolution dans le temps des recaptures par surface de prélèvement. D : durée de séjour. PM, G et Ext : surfaces des prélèvements (voir fig. 1). % L : recaptures dans les surfaces G et Ext, en pourcentage du nombre d'animaux lâchés. % R : mêmes recaptures en pourcentage du nombre total d'animaux recapturés à la même date. An : pourcentage de densité de capture dans la surface PM par rapport à celle dans la surface G pour les non colorés seuls. A : même pourcentage par rapport aux colorés et non colorés ensemble. Rd : rapport entre la densité de recapture dans la surface PM et celle dans la surface PM + G. NG : *N. giardi*. LT : *L. terrestris*. * : donnée indisponible.

lots	D	nombre de recaptures				% R			% L	An	A	Rd
		PM	G	Ext	TOTAL	NG	LT	TOTAL	TOTAL			
CD	22	6	2	0	8	0	29	25	1,8	76	113	1,77
1B	27	26	2	1	29	7	50	10	2,4	58	88	2,19
3A	37	25	4	2	31	22	0	19	9,8	76	108	2,03
1A	39	12	2	6	20	23	71	40	5,8	66	91	2,02
2A	47	53	8	0	61	9	29	13	4,7	87	157	2,05
1C	66	26	5	1	32	19	20	19	5,9	53	73	1,97
2B	73	24	8	14	46	52	42	48	12,7	*	*	1,77
3B	80	4	7	0	11		64	64	15,9	51	54	0,86
1D	120	5	6	1	12		58	58	12,7	48	52	1,07
1E	212	5	0	0	5	0		0	0	89	106	2,35
2C	245	3	0	0	3	0		0	0	58	62	2,35
4A	263	0	0	0	0					96	96	
TOTAL		188	44	25	258							

FIGURE 4 : Densité globale de capture au m^2, par zone de prélèvement. La surface des rectangles est proportionnelle au nombre de captures. Nombres ; *Densités*. ° : l'aire de la surface Ext a été estimée à 1,2 m^2.

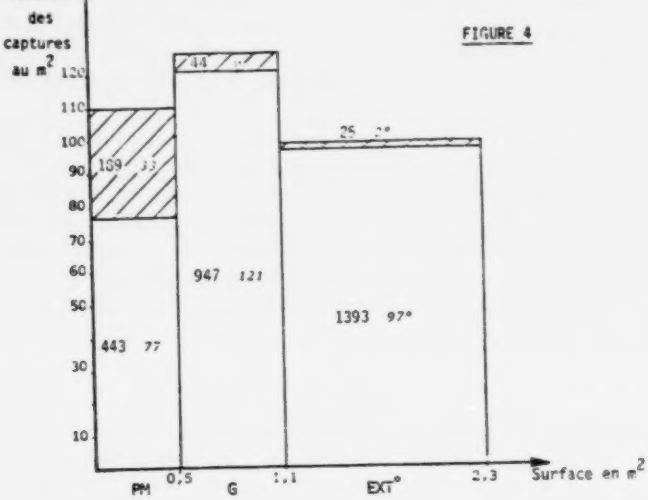


FIGURE 5 : Description schématique de l'évolution dans le temps de la densité de capture dans les surfaces PM et G. (A : rapport entre les densités de capture dans les surfaces PM et G, pour tous les animaux (———) et pour les non colorés (- - - -)). (n : nombre d'individus. d : distance au lieu d'introduction des animaux marqués).

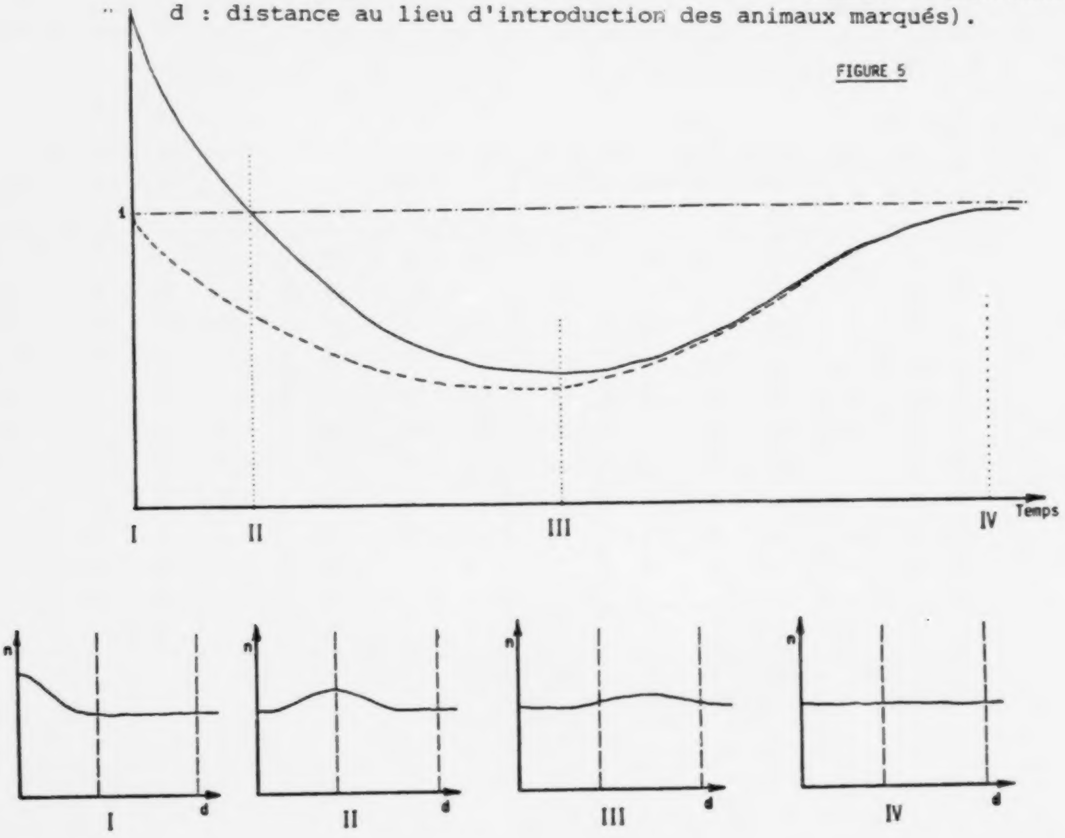


TABLEAU 4

Grignon. Déplacements. Liaisons entre les captures (X1) et le temps (X2). Sp : coefficient de corrélation des rangs de Spearman. D : durée du séjour. C : évolution chronologique des prélèvements. %L : pourcentage par rapport aux lâchés des recaptures dans les surfaces G et Ext. %R : pourcentage par rapport à tous les recapturés de ceux des surfaces G et Ext. %Rg : même pourcentage pour *N. giardi*. A : rapport entre la densité de capture dans la surface PM et celle dans la surface G, pour l'ensemble des animaux. An : même rapport pour les non colorés. ° : significatif au seuil 0,01. * : significatif au seuil 0,05.

X1	X2	Sp	nombre d'observations
%L	D	0,87°	9 (de CD à 1D)
	C	0,87°	
%R	D	0,65*	
	C	0,45	
A	D	-0,69*	8 (de CD à 1D sans le 2B)
An	D	-0,69*	
%Rg	C	0,71*	7 (de CD à 2B)

La densité de capture des animaux non colorés est toujours plus grande dans la surface G que PM (tableau 3, An < 100 %) ; cette différence est significative au seuil de 1 % (test binomial : probabilité critique : 2.10^{-4}). Ces animaux ont donc disparu plus fortement dans la zone de lâcher. Enfin, le rapport A (tableau 3) des effectifs par m^2 des lombriciens capturés (toutes catégories) de PM/G décroît d'abord jusqu'au premier mois, il semble ensuite remonter aux trois derniers prélèvements.

En définitive, l'apport ponctuel d'une population allochtone en surnombre conduit à :
- une migration partielle des allochtones à peu de distance du lâcher,
- une diminution des autochtones au lieu de lâcher,
- un très lent retour à l'équilibre avec une sorte d'onde de déplacement, cette émigration étant probablement accompagnée d'une mortalité induite (cf. Cîteaux) (fig. 5).

Lâcher unique sur une aire : Cîteaux

Les résultats des animaux recapturés dans les carrés de prélèvements sont donnés au tableau 5.

TABLEAU 5

Cîteaux. Nombre d'animaux marqués recapturés dans les carrés des parcelles de prélèvement. TOT : total des recaptures. TOT° : recaptures estimées en tenant compte de la bande médiane de l'aire d'accueil non échantillonnée (voir fig. 2).

	A	B	C	D	E	TOT	TOT°
Nicodrilus Ad.	17	24	3	0	0	44	52,5
Nicodrilus J.	72	48	14	3	4	141	177
Tous *Nicodrilus*	89	72	17	3	4	185	229,5
Tous *Allolobophora*	8	0	0	0	0	8	10
L. castaneus	10	5	4	1	1	21	26
Total général	107	77	21	4	5	214	265,5

La figure 6 donne une image de l'ensemble des animaux recapturés (dans et autour des carrés délimitant les prélevats quantitatifs). On note l'absence de migration des endogés hors de l'aire d'accueil (c'est-à-dire une migration inférieure à 50 cm pendant l'expérience). On constate aussi une recapture plus forte dans les carrés A ou les émigrations sont mieux compensées par des immigrations que dans le carré de bordure B. En utilisant toutes les données de recapture au dehors de l'aire de lâcher on peut constater (fig. 7) un retard à la migration due probablement à l'effet hivernal sauf pour *L. castaneus* et deux *Nicodrilus* juvéniles. Le calcul de la vitesse de migration des pionniers observée peut être tentée (tableau 6) pour les *Nicodrilus*. Ces vitesses, à partir de l'aire d'accueil, ne préjugent pas du trajet effectivement parcouru par les animaux, il s'agit donc de la vitesse minimale calculée sur la distance maximale observée.

L'évolution des captures des animaux non marqués dans l'aire de prélèvement pendant la période d'échantillonnage indique une diminution constante de l'effectif estimé (y) en fonction du temps en jours (x) à partir de fin février ($y = -15,7\ x + 0,33$), la diminution de 1,57 individus/jours/m^2 est significativement différente de 0 au seuil de 0,01. Le rapport formol/formol-bêche est relativement constant sauf en juin lorsque la sécheresse limite l'efficacité de la méthode au formol. En hiver, les basses températures (2 à 4 °C) ont contribué à limiter les captures par toutes méthodes. En dehors des deux premiers prélèvements hivernaux (froid) et du dernier prélèvement estival (sécheresse) la métho-

FIGURE 6 : Nombre total d'individus recapturés au cours de l'étude, par carré de prélèvement.

FIGURE 6

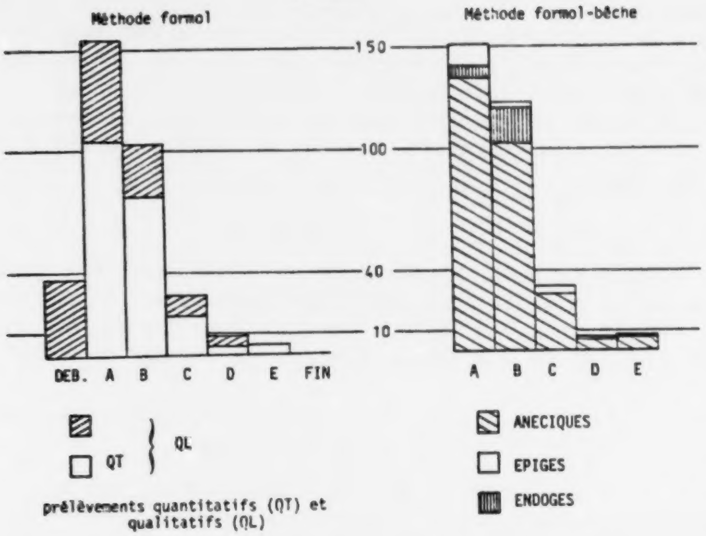
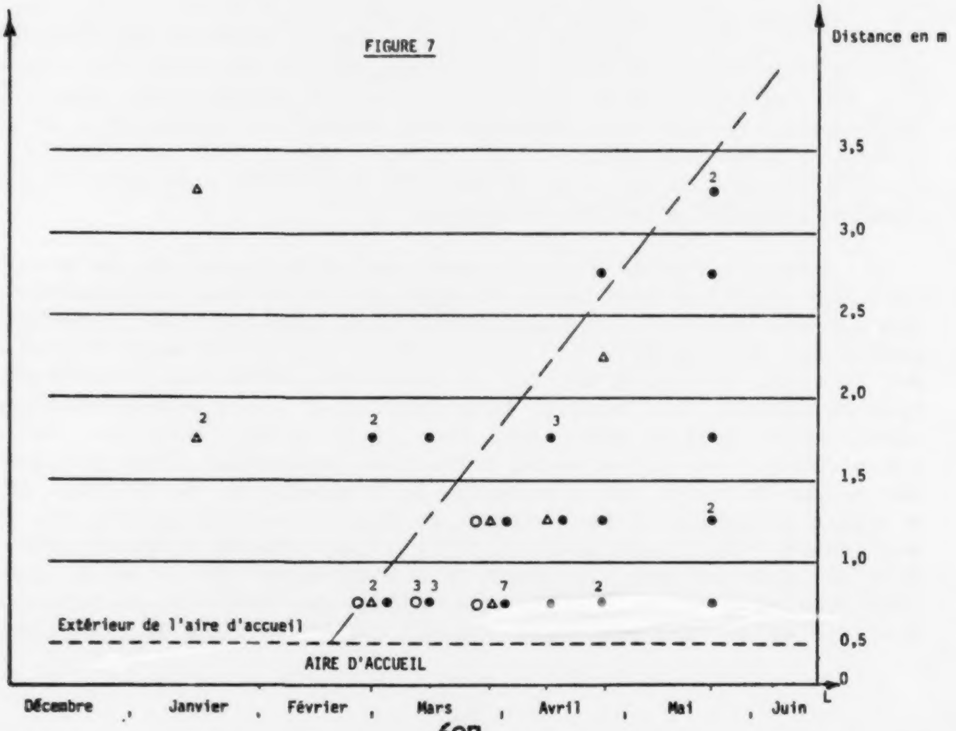


FIGURE 7 : Emigration à Cîteaux. Nombre d'individus recapturés par zone de prélèvement externe (chaque zone est symbolisée par une bande horizontale). ○ : *Nicodrilus* anéciques adultes. ● : *Nicodrilus* anéciques juvéniles. △ : *L. castaneus*. Lorsque le nombre n'est pas indiqué, il n'y a pas de capture. L : ligne de lâcher la plus externe dans l'aire d'accueil.



de au formol s'est avérée d'une efficacité stable pour les vers autochtones et nous admettrons pour les colorés que pendant cette période favorable les résultats n'ont pas été biaisés par la méthode de prélèvement. Nous présentons fig. 8 le pourcentage par rapport au lâcher initial de recaptures des animaux marqués dans la zone ayant reçu uniquement les anéciques (Za) et celle ayant reçu anéciques et autres vers marqués (Zt) (86 % des recaptures sont celles d'anéciques). Le test de Wilcoxon-Mann-Witney nous permet de montrer que la différence de recapture entre les deux séries est significative (à 5 %) en admettant une évolution linéaire avec le temps.

TABLEAU 6

Vitesse (v) minimale de déplacement de pionniers. D : durée de séjour sur le terrain. d : distance minimale parcourue (du milieu du carré B au carré de recapture). + : valeur obtenue dans le cas où on admet que la migration n'a débuté que début février en raison du froid hivernal.

	D en jours	mois de recapture	d en m	v en m/mois
L. castaneus	48	Janvier	3	2
Nicodrilus	175	Mai	3	0,5
	91	Fevrier	1,5	1,5$^+$

Le peuplement recapturé baisse de façon significative avec le temps (fig. 9) pour le peuplement total (régression linéaire significative au seuil 0,05). L'effectif des animaux recapturés est à peu près le même dans les deux aires d'accueil et le nombre d'animaux qui réussissent à se maintenir semble donc dépendre des paramètres écologiques de l'aire d'accueil assez homogènes entre les deux zones. Pour les *Nicodrilus* seuls l'évolution des zones Za et Zt est bien distincte ; la zone la plus surpeuplée présente moins de recapture.

Ainsi, c'est le niveau global des allochtones qui se stabilise mais non celui des espèces ou catégories écologiques allochtones, ce qui indiquerait une certaine compétition interspécifique des lombriciens cohabitants. Cela rejoint les travaux de l'un d'entre nous (Bouché, 1972) sur la faune française mettant en oeuvre le coefficient d'exoécie permettant de mesurer une "égalité de compétition" entre espèces différentes cohabitantes dans un même lieu. Sans avoir la même fonction, les lombriciens cohabitant, appartenant à diverses catégories, sont partiellement inter-compétiteurs. Sur l'ensemble de l'expérience de Cîteaux, il a été possible d'établir le pourcentage de lombriciens recapturés par rapport aux lâchés (peuplement total ≃ 17 %) : les endogés *Allolobophora* répondent mal à la méthode au formol (≃ 6 % de recapture) ; les *L. castaneus* très mobiles "quittent" rapidement l'aire de recapture en raison de leur mobilité et de leur vie brêve (Bouché, 1977) (≃ 18 % de recapture) ; en-

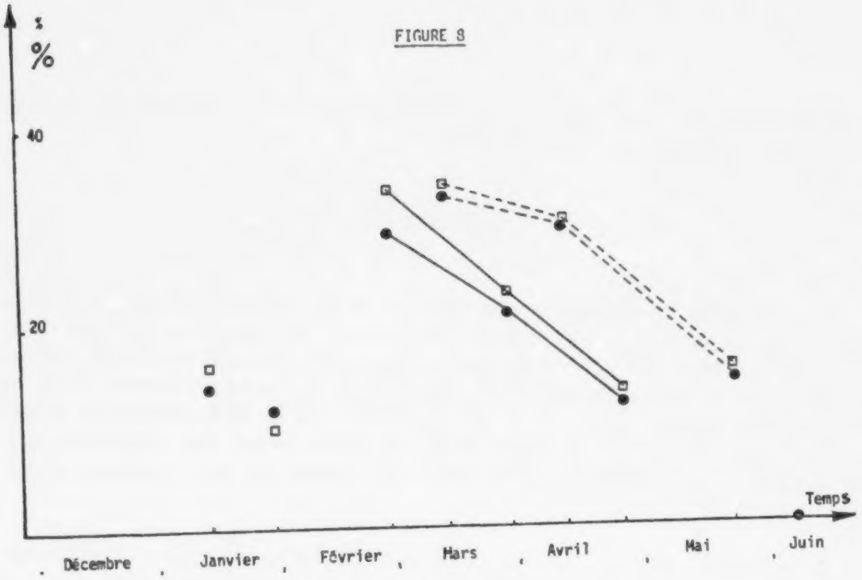


FIGURE 8 : Cîteaux. Pourcentage de recapture par rapport au nombre d'animaux lâchés (méthode formol quantitative). □ : tous *Nicodrilus* anéciques. ● : tous animaux. Zone Zt : traits pleins. Za : tirets.

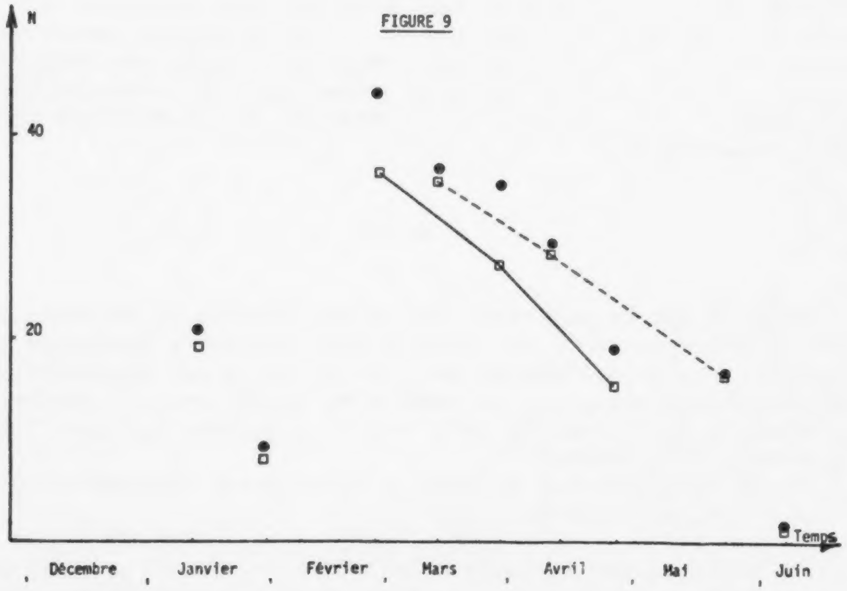


FIGURE 9 : Cîteaux. Nombre de vers marqués recapturés par la méthode formol quantitative. □ : tous *Nicodrilus* anéciques. ● : tous animaux. Zone Zt : traits pleins. Zone Za : tirets.

fin, les *Nicodrilus* anéciques présentent dans leur ensemble un taux meilleur (≃ 19 %) que la moyenne générale.

CONCLUSION

La méthode de marquage-recapture pratiquée à titre d'essais à Grignon et Cîteaux a été d'un emploi difficile surtout en raison des aléas climatiques et des difficultés techniques d'échantillonnage. Le marquage par coloration s'est montré satisfaisant ; il a été réussi avec quatre colorants dont trois ont servi au terrain. Il a été possible d'observer des migrations ; celles-ci sont très faibles chez les endogés, au maximum de l'ordre de 1 m/mois pour les anéciques et de 2 m/mois chez les épigés.

A Grignon, les *L. terrestris* ont migré plus que *Nicodrilus giardi* et *Allolobophora icterica*. A Cîteaux, les *L. castaneus* ont migré rapidement par rapport aux *Nicodrilus* anéciques tandis que les *Allolobophora* furent apparemment très stables : la vitesse de migration épigés > anéciques > endogés est conforme aux moeurs de ces catégories écologiques.

En raison du caractère sédentaire des animaux, l'état de surpopulation a entraîné des effets sur les autochtones et allochtones. Ceux-ci migrent sur quelques décimètres, fuyant la zone de surpopulation initiale à la manière d'une vague concentrique (Grignon) et une différence de 8 % en effectif (Cîteaux) entraine un taux de recapture plus faible dans la parcelle à forte surpopulation (24 %). Cette surpopulation, due à des endogés et épigés, affecte également les recapturés des anéciques. La réduction de la surpopulation se fait à la fois par élimination d'autochtones et d'allochtones. Ce n'est pas au niveau de chaque espèce ou mieux de chaque catégorie écologique que l'équilibre après une surpopulation allochtone colorée se fait après le lâcher mais au niveau de l'ensemble du peuplement : ceci illustre la compétition interspécifique entre lombriciens cohabitants.

RESUME

Dans le but de maîtriser les divers aspects du marquage par coloration (en rouge ou vert) des lombriciens, une étude technique a été conduite. Les lombriciens marqués ont été ajoutés à des peuplements naturels et les évolutions spatiales et pondérales furent suivies pendant plusieurs mois. Parmi la multitude des informations acquises, quelques traits dominants peuvent être dégagés :

1) la surpopulation accroît la disparition (mortalité ou émigration) au terrain,
2) cet effet affecte tout le peuplement indépendament de l'espèce ou du groupe écologique introduit (compétition interspécifique),
3) après installation, les lombriciens migrent généralement peu (moins de 50 cm) tandis que certains pionniers franchissent quelques mètres,
4) l'aptitude aux deux types de migration varie avec les catégories écologiques.

Ces nouvelles techniques peuvent être utilisées pour les études de taux de mortalité, d'accroissement de biomasse, de migrations èt de faisabilité de la biostimulation des sols par l'introduction de lombriciens.

SUMMARY

Overpopulated introductions and migrations of labelled earthworms.

In the aim to improve new techniques to label earthworms, research on those techniques was made and led to the coloration of animals in red and green by stainning. Such labelled earthworms were introduced in field in addition to the original communities. Migrations and weight evolutions of both labelled and unlabelled earthworms were followed during months. Among a lot of observations some main facts were noticed :

1) overpopulation increases disapearence (mortality or migration) in field,
2) this overpopulation harms all the community without respect of the introduced species or ecological group (interspecifiç competition),
3) migration of settled earthworms is very limited in space (below 50 cm) for must earthworms while some pioneers migrate far away (few meters),
4) width of both migration types depends of ecological groups.

These techniques would be used to study mortality rates, biomass increments, migration and feasability of soil improvment by earthworm introductions.

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SESSION IX: BASIC SOIL ECOLOGY: SOIL ECOLOGY OF THE ARCTIC AND DESERTS, STRUCTURE AND FUNCTION OF SOIL ORGANISM COMMUNITIES

Moderator: M. B. Bouché

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INFLUENCE OF INDIVIDUAL PLANT SPECIES ON THE DISTRIBUTION OF ARCTIC COLLEMBOLA

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INTRODUCTION

The macroflora is generally considered to effect collembolan populations indirectly, by modifying the microclimate, soil structure or microbial populations (e.g. Strickland, 1947; MacFadyen, 1954; Knight, 1961). Christiansen (1964) pointed out that the importance of the macroflora as a factor influencing collembolan distribution is reflected in the fact that there is generally at least a moderate degree of correspondence between plant and collembolan associations.

Direct effects of the macroflora on collembolan populations have also been postulated. Müller (1959) demonstrated that the living plant root systems of individual plant species influenced the distribution of Collembola in a wetland soil, and although he was unable to determine the cause, he was able to show that the plant root system must be alive to exert this effect. Many Collembola show distinct feeding preferences, and will selectively feed on certain species of leaves (Dunger, 1962) plant roots (Winner, 1959) or fungi (McMillan, 1976; Addison and Parkinson, 1978). Biologically active substances secreted by plants have also been shown to influence different collembolan species. (Palissa, 1967; Müller and Chou, 1972).

In spite of the overwhelming evidence for both direct and indirect effects of the macroflora on collembolan distribution, there is little evidence for the restriction of individual collembolan species to the immediate vicinity of any one plant species (Christiansen, 1964.) More recently Blackith (1974) suggested that in poorer soils ("tundra-type soils"), where energy and nutrient input are limited, Collembola may be more closely tied to the immediate vicinity of a plant than in soils such as arable or woodland soils which contain sufficient decomposing material to allow them to live away from the plant root and stem system. Based on his own work in an Irish blanket bog, and evidence from the non-English literature, he also suggested that Collembola choose plant root systems on a host-specific basis.

The purpose of this study was to investigate the relationship between individual vascular plant species and their associated collembolan faunas. The study was carried out in the high arctic region of Canada, in areas with generally sparse vegetation cover.

Under these conditions it was easy to obtain "pure" samples from the different plant species since each individual plant (including its root system) was distinctly separate from any other vascular plant. The Collembola associated with the following four species of vascular plant were studied: *Saxifraga oppositifolia* L., *Saxifraga caespitosa* L., *Dryas integrifolia* M. Vahl, and *Luzula confusa* Lindeb. Samples were collected from three different islands in the Northwest Territories in Canada; Devon Island, Cornwallis Island and King Christian Island. Two different plant communities were sampled on Devon Island, giving a total of four sites in all.

SITE DESCRIPTIONS

Devon Island - Beach Ridge (DBR)

A cushion plant/lichen community was associated with this site. Vascular plant cover was <20%, lichens covered approximately 60% of the area, and 20% was entirely bare (Svoboda, 1977). The soil at this site was a Regosolic Static Cryosol (Walker and Peters, 1977).

Devon Island - Transition Zone (DTZ)

A cushion plant/moss community was associated with this site. Vascular plants covered nearly 60% of the area, with lichens and moss making the total plant cover up to 100%. The soil was classified as a Brunisolic Static Cryosol (Walker and Peters, 1977).

Cornwallis Island (CI)

Samples were taken from a cushion plant and lichen covered area approximately 1.5 km NNW of the north end of the runway at Resolute Bay. Vascular plant cover was <10%, and the soil was described by Cruickshank (1971) as a "shallow polar desert soil."

King Christian Island (KCI)

A lichen-moss-rush community was characteristic of the site. Vascular plants covered only 8.7% of the area, and 33.2% of the soil was unvegetated. The soil was a Regosolic Static Cryosol (Addison, 1977).

Using the nomenclature of Bliss et al. (1973), the sites on King Christian Island, Cornwallis Island, and the Beach Ridge site on Devon Island would all be classified as polar-semi-desert areas (2-20% vascular plant cover), whereas the Devon Island Transition Zone Site would be classified as a tundra site (>20% vascular plant cover).

METHODS

Ten replicate cores ($23.75\ cm^2$ x 7.5 cm deep) were taken from each plant species at each site in which it occurred. In addition, ten cores of soil from non-vegetated areas approximately 15 cm from S. oppositifolia plants were taken from the Devon Island Beach Ridge Site, and a similar series of samples was taken on King Christian Island, approximately 75 cm from L. confusa.

Each core was divided into three 7.5 cm sections, and the Collembola were extracted in a high gradient extractor modified from MacFadyen (1962).

All the Devon Island samples with the exception of those from S. caespitosa and L. confusa were collected in August 1974, and were extracted on site. Samples from Cornwallis and King Christian Island were taken in August 1975, and were shipped south to Edmonton, Alta. before the Collembola were extracted. The Devon Island S. caespitosa and L. confusa samples were obtained in August 1978 and were also extracted in Edmonton.

RESULTS

Effect of vascular plant cover on abundance of Collembola

A comparison of the numbers of Collembola obtained from soil samples with and without vascular plant cover (Table 1) shows that in both the Devon Island Beach Ridge and the King Christian Island Site, Collembola were much more abundant in samples containing a vascular plant than in samples of bare soil.

TABLE 1. Influence of vascular plant cover on abundance of Collembola. Means based on 10 samples.

Site	Vascular Plant	Mean no. Collembola/ sample (95% confidence limits)
Devon Island-Beach Ridge	Saxifraga oppositifolia	51 (36.1-65.9)
	Bare soil	11.5 (4.9-18.0)
King Christian Island+	Luzula confusa	75.8 (52.2-99.4)
	Bare soil	4.6 (0.0-10.1)

+ statistical comparison of 2 sample types from KCI not strictly valid since variances are unequal.

Effect of individual plant species on collembolan communities

The collembolan faunas of the twelve microsites (plant-site combinations) were compared using the Cornell version of the Bray-Curtis Ordination technique (Computer Programs CEP40 and CEP50 (Gauch, Lanyon and Whittaker, 1971)). These programs use two indices of similarity: coefficient of community (Sorenson, 1948) and percentage similarity (Gauch and Whittaker, 1972). The former index uses qualitative (presence and absence) data only while the latter incorporates both qualitative and quantitative information. The results of these analyses are shown in Figures 1 and 2. Regardless of which similarity index was used in the ordination, the microsites clustered out in groups according to site (or plant community). There was absolutely no tendency for the microsites to cluster according to plant species.

The modified version of the Bray-Curtis Ordination Technique was also used to express the degree of similarity between the collembolan faunas of different plant species at the same site. In all cases there was considerable overlap in the ordination of the individual samples, and groups of points representing the faunas of individual plant species could not be identified.

Effect of individual plant species on abundance of Collembola

Although in general the species composition of the Collembola taken under different plant species at the same site was similar, evidence of within site selection of certain plant species over others can be seen by considering the abundance of Collembola under the different plant species (Table 2). Differences in the abundance of Collembola under different plant species are especially evident in the polar semi-desert sites (<20% vascular plant cover). The species of plant containing the highest numbers of Collembola varied according to site, so no one species could be identified as providing the most favourable habitat for Collembola.

Effect of individual plant species on distribution of collembolan species

The distribution of collembolan species in relation to individual plant species is shown in Appendix A. One species (*Folsomia regularis*) occurred under all plant species at all sites, but no species of collembole could be linked with a particular species of plant regardless of its site. Several species were found only at one site or one island (e.g. *Tullbergia simplex* - DBR; *Folsomia elongata* - CI). Although *Vertagopus* sp. nr *brevicauda* was collected only from under *S. caespitosa* on Cornwallis Island in 1975, this species occurred under both *S. oppositifolia* and *L. confusa* as well as *S. caespitosa* on King Christian Island. In fact it was also found in samples of *S. oppositifolia* from an unidentified plant community near Resolute Bay, Cornwallis Island in 1978. These samples also contained specimens of *Willemia* sp., a species that was absent from all samples of *S. oppositifolia* taken in 1975.

FIGURE 1. Bray-Curtis Ordination of microsites (plant-site combinations), based on Coefficient of Community. ● *S. oppositifolia*, ▲ *S. caespitosa*, ■ *D. integrifolia*, ◆ *L. confusa*.

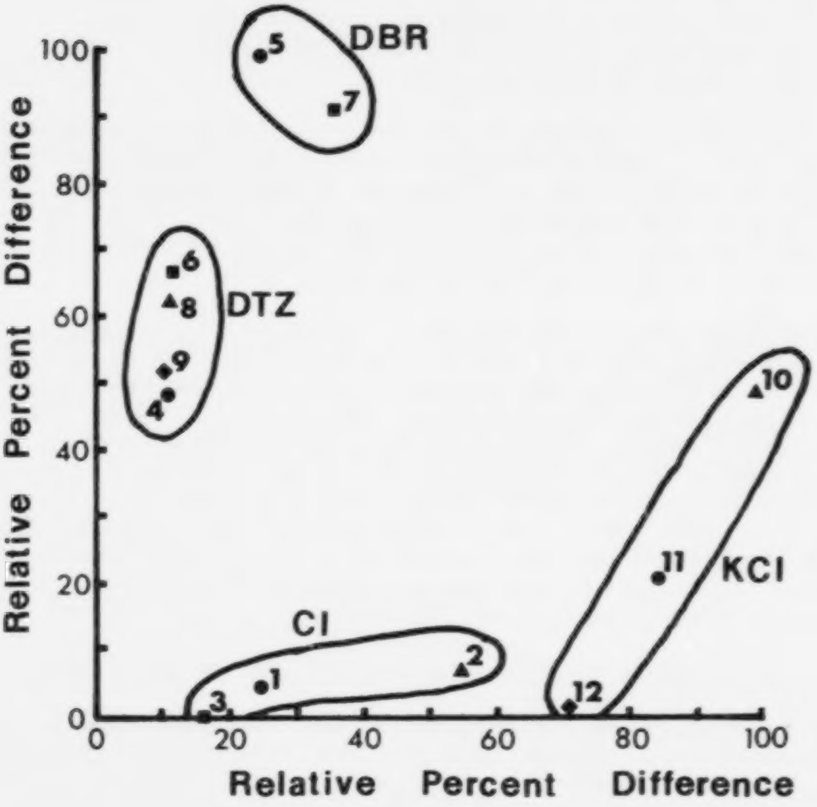

FIGURE 2. Bray-Curtis Ordination of microsites (plant-site combinations), based on Percentage Similarity.

● *S. oppositifolia*, ▲ *S. caespitosa*, ■ *D. integrifolia*, ♦ *L. confusa*.

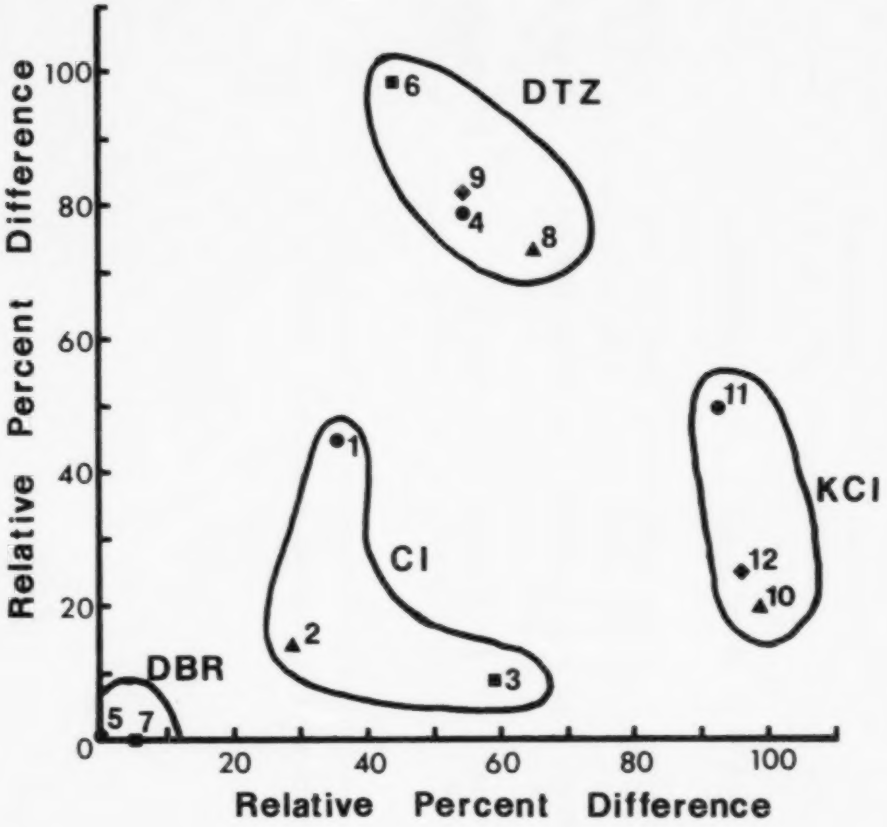

TABLE 2. Mean number of Collembola per sample (23.75 cm^2). Means not underscored by the same line differ at the 0.05 level using a Student Newman Keuls Multiple Range Test.

Site		Mean no. Collembola/sample			
Devon Island- Beach Ridge	Plant	*D. integrifolia*	*S. oppositifolia*		
	$\bar{x}$	28.1	51.0		
Transition Zone	Plant	*D. integrifolia*	*S. oppositifolia*	*S. caespitosa*	*L. confusa*
	$\bar{x}$	15.3	25.5	36.8	40.0
Cornwallis Island+	Plant	*S. oppositifolia*	*D. integrifolia*	*S. caespitosa*	
	$\bar{x}$	20.6	41.1	88.9	
King Christian Island+	Plant	*S. oppositifolia*	*L. confusa*	*S. caespitosa*	
	$\bar{x}$	61.1	84.9	121.0	

+ $\log_{10}(x + 0.5)$ transformation of original data used. Derived means shown.

DISCUSSION

The results of this study (Table 1) indicate clearly that in impoverished soils Collembola are indeed closely tied to the immediate vicinity of a plant species as suggested by Blackith (1974). Similar results were obtained by Seniczak and Plichta (1978), who compared the numbers of oribatid mites in soils with a cover of lichen, moss, and S. oppositifolia and found the mites were most abundant under S. oppositifolia.

Attempts to link collembolan communities or individual collembolan species with individual plant species failed. In comparing the collembolan faunas of different islands, zoogeographical considerations must obviously be taken into account. The absence of a species on a particular island can be attributed to one of two factors; that the species near reached the area, or that having reached the area it was unable to maintain itself in sufficiently high numbers to be taken in the samples. Whatever the reason, many species of Collembola simply did not occur on some of the islands, so that their absence under a particular plant species at such a site is not strictly comparable to an absence under a plant at a site at which it was present. In general the species composition of the Devon Island fauna resembled those of Northern Greenland (Hammer, 1954) and Ellesmere Island (Hammer, 1953), and was quite distinct from the collembolan fauna of King Christian Island. Cornwallis Island contained elements from both the eastern arctic (Devon Island) fauna and that of the western arctic (King Christian Island).

This study also failed to detect specific plant-collembole associations within a single island. The collembolan faunas of S. oppositifolia and D. integrifolia at the Devon Island Beach Ridge Site were very similar to one another, and very different from the fauna of the same plant species in a different plant community a mere 10 m away. It was expected that if species of Collembola were attracted by some characteristic of a particular plant species, such as root exudates, the rhizosphere flora, or characteristics of the organic matter, then these Collembola would be found in close proximity to the same plant, regardless of the plant community. It should be remembered however, that the various characteristics of specific plants mentioned above might themselves be altered by characteristics of the different sites and so differ in their ability to influence Collembola.

The conclusion that Collembola were associated with a particular plant community rather than a particular plant species differs from that of Blackith (1974). The results of the present study are in agreement with those of Curry (1976) who found that although herbivorous species appeared to discriminate between host plant species, it was not possible to differentiate between samples on the basis of detritivorous species.

In this study differences between the numbers of Collembola under different species of plants were demonstrated. Stebaeva (1963) suggested one possible way in which different plant species might affect collembolan abundance. She reported that Collembola were more numerous and were found at lower depths under plants with deeply penetrating root systems than under shallow-rooted plants. This however cannot account for differences observed in the present study since the root systems of all species penetrated at least 7.5 cm, but 75-90% of the Collembola were extracted from the top 2.5 cm of soil with, <5% occurring below 5 cm.

The most likely explanation for the fact that Collembola were more abundant under certain plants than others is that their abundance was related to the growth form of the plant. At the Beach Ridge Site on Devon Island, S. oppositifolia had short internodes and formed compact cusions that would trap snow in winter, and within which organic matter would accumulate. The water holding capacity and hence humidity could be expected to be higher here than in the surrounding area (Svoboda 1977). At this site D. integrifolia plants formed a loosely structured mat, of which most of the surface was dead. It is likely that Collembola would prefer the compact cusion plant growth form of S. oppositifolia to the growth form exhibited by D. integrifolia. At the Devon Island Transition Zone, S. oppositifolia had long internodes and its growth form resembled that of a prostrate shrub (Svoboda 1977). This latter growth form was also exhibited by S. oppositifolia on the sites sampled on Cornwallis and King Christian Island. This growth form would not be as attractive to the Collembola as a dense cushion plant. S. caespitosa always exhibited a compact cushion plant growth form, perhaps explaining why this species always contained high numbers of Collembola. Collembola were also abundant under L. confusa, which formed a dense mat rather than a cushion plant. This plant species was only found in less exposed parts of the sites; areas with good snow cover in winter (Addison, 1977). These areas would be expected to contain high numbers of Collembola regardless of the species composition of the vascular plant cover.

The lack of host-specificity in arctic Collembola is not surprising. Environmental conditions are so harsh, and nutrient and energy inputs are so low, that from an evolutionary point of view, an organism cannot afford to become too specialized. It must be able to tolerate a wide range of environmental conditions and utilize different food sources and microhabitats for survival. As Savile (1960) pointed out, in environments where abiotic factors are of such over-riding importance, biotic interactions between species may often be of little consequence. It is suggested that if host-specificity amongst Collembola does in fact occur, it is more likely to be found in more temperate areas than in the impoverished soils of the Arctic.

CONCLUSIONS

Collembola were more abundant in soil samples with vascular plant cover than in bare soil. Although Collembola were sometimes more abundant under certain plant species than others, the species of plant was apparently not as important as its growth form.

In general, species of Collembola could not be linked with a particular species of vascular plant. The collembolan faunas under different plant species within a single plant community were very similar, and differed considerably from the faunas of the same plant species in a different plant community on the same island. Differences in the composition of the collembolan fauna of different islands were greater than intra-island (habitat) differences.

It was concluded that zoogeographic and microclimatic considerations were more important than the species composition of the macroflora in determining the distribution of Collembola in the High Arctic.

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Appendix A. Distribution of collembolan species on Devon Island, Cornwallis Island and King Christian Island, N.W.T., in relation to individual plant species.

	% total no. individuals at each microsite											
	DEVON ISLAND						CORNWALLIS ISLAND			KING CHRISTIAN ISLAND		
	Beach Ridge		Transition Zone									
	Saxifraga oppositifolia	*Dryas integrifolia*	*Saxifraga oppositifolia*	*Saxifraga caespitosa*	*Dryas integrifolia*	*Luzula confusa*	*Saxifraga oppositifolia*	*Saxifraga caespitosa*	*Dryas integrifolia*	*Saxifraga oppositifolia*	*Saxifraga caespitosa*	*Luzula confusa*
Hypogastrura tullbergi (Schäffer)	87.1	81.9	19.1	13.5	17.5	12.7	46.5	81.3	20.9			
Hypogastrura sp. nova										9.2	11.4	9.1
Anurida granaria (Nicolet)									0.4			
Micranurida pygmaea Börner			0.6									
Willemia sp.		0.3							6.7			
Onychyiurus groenlandicus (Tullberg)			0.3	1.3		1.9	0.2	0.6	0.1			0.4
Tullbergia simplex ? Gisin	2.1	3.8										
Stachanorema sp.	4.0		5.3	1.1	18.2	5.5						
Folsomia regularis Hammer	2.3	7.3	71.3	80.4	55.8	60.1	51.2	10.3	58.4	58.3	71.5	70.1
F. quadrioculata (Tullberg)	0.2			0.8								
F. bisetosa Gisin	4.2	5.2				6.0						
F. duodecimsetosa Hammer				0.3								
F. elongata MacGillivray							0.7	1.7	9.8			
Isotoma violacea Tullberg			0.3		2.6	7.4			0.1			
I. palustris (Müller)				2.4	2.6	2.7						
I. ekmani Fjellberg				0.3	2.6	3.0						
I. viridis group							0.7	0.3	1.6			
I. sp.			2.9		0.7	0.2						
Vertagopus sp. nr *brevicauda* Carpenter								5.9		32.4	17.1	16.9
Entomobrya comparata Folsom	0.2	1.3										
Megalothorax minimus (Willem)						0.5	0.7		1.9	0.2		3.4
Total no. individuals in 10 samples	510	281	255	368	153	400	432	1,424	796	654	1,337	909

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DISTRIBUTION AND DIVERSITY OF NORTH AMERICAN ARCTIC SOIL ACARI

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INTRODUCTION

In the arctic, as in all ecosystems, various environmental factors are interrelated, changes in one causing changes in others. Rate of nutrient turnover and subsequent rate of primary productivity are dependent primarily on microorganism activity. This, in turn, is limited by food, space, dispersal, cropping, biostasis and senescence (Hinshelwood, 1951). These effects are, however, counteracted by the activities of soil animals, such as mites. Mites not only serve as catalysts for microorganism activity (Edwards and Heath, 1963; Crossley and Witkamp, 1964; Macfadyen, 1968) but also constitute an important mineral reservoir (Hudig, 1949; Webb, 1977).

Yet prior to Hammer's (1952) monograph on the Oribatei of northern Canada, the mite fauna of the North American arctic was virtually unknown, except for reports of 16 species from the Queen Elizabeth Islands (MacLachen, 1879; Banks, 1919). Subsequently, Acari were collected from Lake Hazen, Ellesmere Island (Oliver, 1963; Lindquist in lit., 1977); Ellef Rignes Island (McAlpine, 1964, 1965); Baffin Island and Inuvik (Swales, 1966); Bathurst Island (Danks and Byers, 1972); Devon Island (Ryan, 1972, 1973, 1974) and Melville Island (Lindquist in lit., 1977). Literature on these studies stresses the low species diversity in the arctic.

Soil acarine studies in the Alaskan arctic were initiated by Hammer's (1955) major study on the Oribatei of Point Barrow and subarctic forests. Subsequently, mites of the coastal tundra around Point Barrow were intensively studied by Hurd (1958), Strandtmann (1967), Bohnsack (1968), MacLean (1971, 1975), Douce (1973, 1976) and Douce and Crossley (1977). Soil mites of Cape Thompson were also studied following a proposal by the U.S. Atomic Energy Commission to build a deep-water port there (Watson, Davis and Hanson, 1966).

These studies revealed differences between acarine faunas of arctic and temperate soils. Life-forms in the arctic are associated with soil surface, litter and moss cover, deep forms and arboreal species being absent (Douce, 1973). It appears that Collembola play a more significant role relative to mites in tundra than in other ecosystems (Douce and Crossley, 1977). Mites predominate in organic substrates, whereas mineral soils support higher densities of Collembola (Watson et al., 1966). In coastal tundra, around Point Barrow, density and diversity of Prostigmata is greater than that of other acarine groups (Douce and Crossley, 1977). This contrasts with most temperate regions where Oribatei generally predominate in undisturbed soils (Wallwork, 1976).

In the past 12 years interest in arctic and subarctic ecosystems has greatly increased with the exploitation of oil, gas and mineral reserves in these regions. Yet data concerning acarine species diversity are scant. In view of the importance of soil mites it was relevant to determine, in greater detail, their distribution and diversity in the North American arctic and subarctic and changes in their distribution and diversity along a latitudinal gradient from subarctic to polar desert.

Site Descriptions

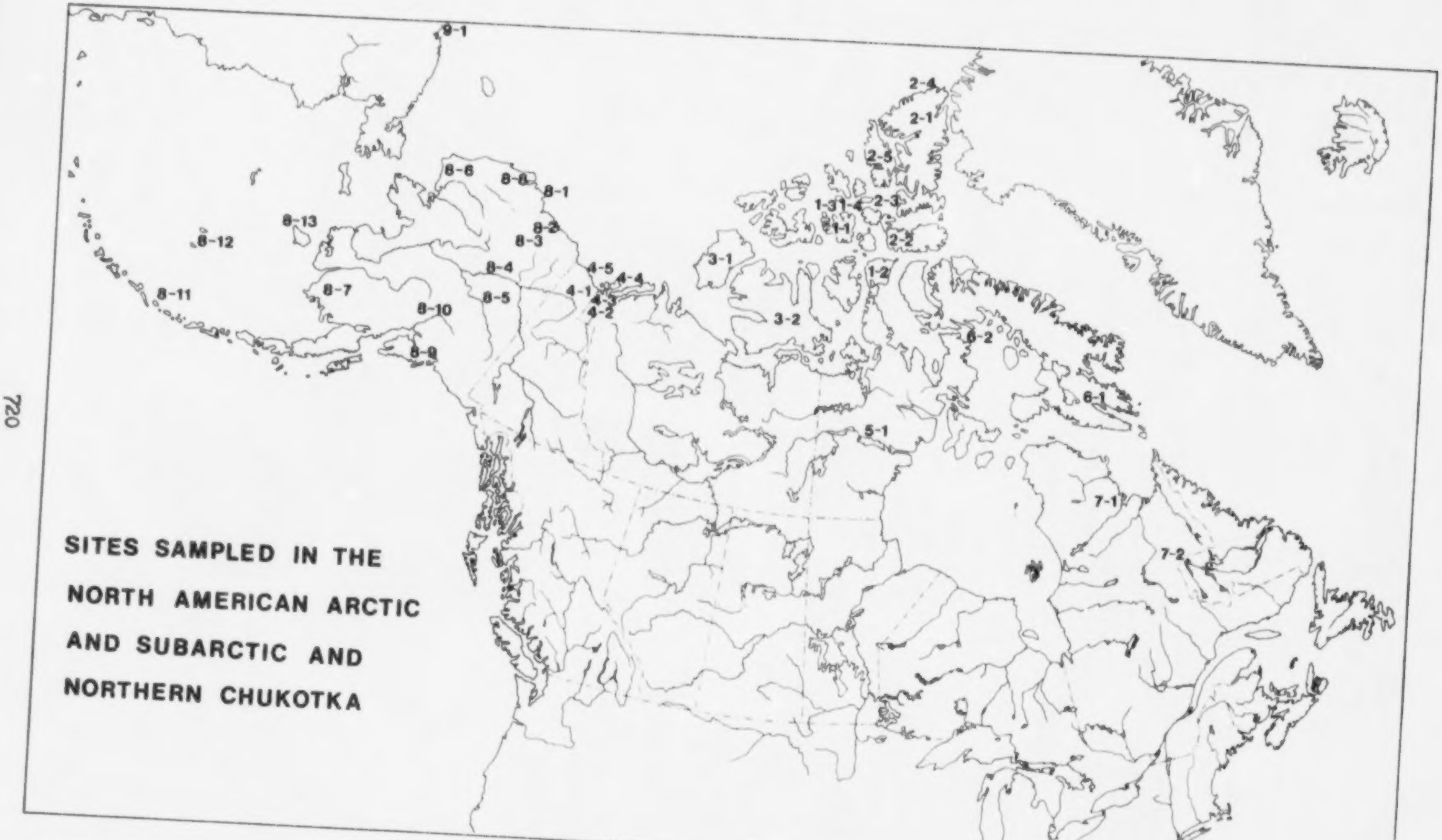
From 1970 to 1976, 833 soil samples were collected from 34 major sites in the North American arctic and subarctic (Table I, Figure 1). Of these, 698 were from arctic and 135 from subarctic areas. The Canadian samples were assigned to seven geographical regions following the terminology of the Canadian Committee for the Terrestrial Conservation Section of the International Biological Program (Nettleship and Smith, 1975). Sites in Alaska were, for simplicity, placed in one geographical region. Eleven soil samples were collected from Chaun Bay, northern Chukotka, U.S.S.R. in 1975. Data from these samples, discussed by MacLean, Behan and Fjellberg (1978), are compared with results from the North American arctic in the present study.

A brief description of the location, ecology and climate of each site, with a list of species collected is given in Behan (1978). Previous data on acarine diversity were available for only nine of the 34 sites sampled; Bathurst Island (Danks and Byers, 1972); Ellesmere Island (Oliver, 1963; Lindquist in lit., 1977); Devon Island (Ryan, 1972, 1973, 1974); Yukon Territory and MacKenzie Delta, subarctic (Hammer, 1952); Alaska, northern coastal plain (Hammer, 1955; Hurd, 1958; Strandtmann, 1967; Bohnsack, 1968; MacLean, 1971; Douce, 1973, 1976); Brooks Range and Fairbanks Region (Hammer, 1955) and Northwest coastal area (Watson et al., 1966).

Table 1. Sampling sites in the North American arctic and subarctic and northern Chukotka, U.S.S.R.

REGIONS	SITES AND ABBREVIATIONS	NO. OF SOIL SAMPLES
Western High Arctic	*1-1 Bathurst Island (BaI)	32
	1-2 Somerset Island (SomI)	12
	1-3 Seymour Island (SeI)	2
	1-4 King Christian Island (KCI)	22
Eastern High Arctic	*2-1 Ellesmere Island (EI)	38
	*2-2 Devon Island (DI)	14
	2-3 North Kent Island (NKI)	2
	2-4 Ward Hunt Island (WHI)	2
	2-5 Axel Heiberg Island (AHI)	2
Western Low Arctic Islands	3-1 Banks Island (BI)	12
	3-2 Victoria Island (VI)	16
MacKenzie District	*4-1 Yukon Territory (YT)	11
	*4-2 MacKenzie Delta - subarctic (MDsa)	10
	*4-3 MacKenzie Delta (MD)	14
	4-4 Tuktoyaktuk Peninsula (Tuk)	14
	4-5 Herschel Island (HI)	6
Keewatin District	5-1 Keewatin District (Ke)	12
Baffin Island Region	*6-1 Baffin Island (BfnI)	107
	6-2 Igloolik Island (IgI)	49
Labrador and Northern Quebec	7-1 Northern Quebec (NQ)	16
	7-2 Labrador - subarctic (Lsa)	7
Alaska	*8-1 Northern coastal plain (Ncp)	64
	8-2 Brooks Range - northern foothills (BRnf)	73
	*8-3 Brooks Range (BR)	36
	8-4 Brooks Range - southern foothills (BRsf)	21
	*8-5 Fairbanks region - subarctic (FR)	44
	*8-6 Northwestern coastal area (NWc)	42
	8-7 Southwestern coastal area (SWc)	15
	8-8 Atkasuk (Atk)	46
	8-9 Kenai Peninsula and Chugach Mountains (CmKp)	18
	8-10 McKinley Park (McKP)	35
	8-11 Aleutian Islands (AI)	29
	8-12 Pribilof Islands (PI)	3
	8-13 Nunivak Island (NI)	7
U.S.S.R.	9-1 Chaun Bay (CB)	11

* Sites from which Acari have been previously collected.


SITES SAMPLED IN THE NORTH AMERICAN ARCTIC AND SUBARCTIC AND NORTHERN CHUKOTKA

9-1
8-6
8-8
8-1
8-2
8-3
8-4
8-5
8-13
8-12
8-11
8-7
8-10
8-9
4-5
4-4
4-1
4-3
4-2
3-1
3-2
2-4
2-1
2-5
1-3
1-4
2-3
1-1
2-2
1-2
6-2
6-1
5-1
7-1
7-2

FIGURE 1.

METHODS

Samples for this study were collected by many arctic researchers and this precluded any overall sample uniformity. Most samples were less than 10cm x 10cm and in any particular habitat a uniform sample size and sampling method were used.

Samples were usually cut with a knife and removed from the ground with a spade, or, less frequently, the ground was sampled with a 5.5 cm diameter corer. In many habitats, for example, screes, talus slopes and high arctic localities, where the active layer is less than 2cm in depth, a handful of this layer was removed. Thus, samples were not directly comparable because of variability in collecting personnel, sampling methods and habitats. Samples were placed in plastic bags immediately after collection and were extracted either immediately, or one to six weeks later, after storage at a cool temperature.

Extraction was carried out in a modified (Hill, 1969; Behan, Hill and Kevan, 1978) Kempson, Lloyd and Ghelardi (1963) apparatus. Each sample was divided into 2.5cm deep subsamples where necessary.

RESULTS AND DISCUSSION

Qualitative Results

Three hundred and ninety-three species of Acari from 87 families were recorded from the 833 samples from the North American arctic and subarctic. These include 181 species of Oribatei from 78 genera, 101 species of Mesostigmata from 40 genera and 111 species of Prostigmata from 45 genera. Of the species recorded 52 were found only in subarctic localities and 95 only in arctic areas. Three species recorded at Chaun Bay, U.S.S.R. (MacLean et al., 1978) were not recorded from the North American arctic - *Eviphis* sp., *Haemogamasus dauricus* and *Haplozetes vindobaenensis*.

Similarity between Acari of Alaska and Canada is greatest among the Oribatei (Table 2). This is probably because the oribatid fauna of the North American arctic is comparatively well known, only 46 undescribed species being recorded, whereas 69 species are undescribed in each of the Mesostigmata and Prostigmata. Previous studies in the North American arctic have recorded 219 species. This study has increased this number to 404 species.

TABLE 2. Similarities between arctic Acari from Nearctic and Palaearctic Regions.

	Acarine Groups		
% Canadian Species Recorded In:	Oribatei	Mesostigmata	Prostigmata
Alaska	69.0%	35.0%	49.0%
Northern and Western Greenland	30.0% (39 spp.)	-	-
Scandanavia	35.6% (46 spp.)	-	-
Soviet Union arctic	39.0% (50 spp.)	-	-
% Alaskan Species Recorded In:			
Northern and Western Greenland	27.5% (41 spp.)	-	-
Scandanavia	33.0% (49 spp.)	-	-
Soviet Union arctic	42.0% (63 spp.)	-	-

The oribatid fauna of both the Canadian and Alaskan arctic more closely resembles that of the Soviet arctic than that of Scandanavia or northern Greenland (Table 2). At the present time, data concerning Mesostigmata and Prostigmata are inadequate to make similar comparisons.

The western arctic, comprising the Alaskan arctic and arctic regions of the Yukon Territory and MacKenzie Delta, supports a more diverse mite fauna (331 species) than the eastern arctic (199 species). This may be explained by: a) the northerly extension and island pattern of the eastern arctic that have presented difficulties to post-glacial invasion by Acari; b) treeline sweeps far to the north in the west, e.g., in the MacKenzie Delta it reaches 69°50'N. In the eastern arctic treeline is found as far south as 60°N and the arctic archipelago is treeless; c) there is strong biological and geological evidence for the presence of ice-free areas in north and central Alaska during the two most recent glaciations, the Illinoian and Wisconsin (Ives, 1974; Matthews, 1975).

Diversity of arctic acarine genera and species between sites

Certain genera are strongly represented in the arctic in comparison with other genera, more so than could be expected if the arctic fauna is solely a reduced southern fauna, as hypothesized by Downes (1965) for insects. Eleven species of *Arctoseius*, 12 species of *Epidamaeus*, and 5 species of *Trichoribates*, occur in the arctic. This suggests that these genera were particularly capable of adapting to post-glacial conditions.

The family Arctacaridae was first described from Point Barrow, Alaska (Evans, 1955). As two other species have been described from the eastern Soviet Union (Gilyarov and Bregatova, 1977) this family may have an east Asian or Beringian origin. In this study its distribution is restricted to the western arctic and subarctic, other than a single record from Keewatin District. Absence of this family from the arctic islands is probably a result of distributional rather than environmental difficulties, as its abundance at Point Barrow suggests that it is able to survive in the high arctic.

Iugoribates gracilis, previously unrecorded from northern Canada, has been recorded from almost all sites, particularly those with high arctic or polar desert environments.

The genera *Ceratoppia*, *Metrioppia* and *Pyroppia* (Family Metrioppiidae) are well represented in the western arctic, particularly in Alaska. The latter two genera have no representatives in the eastern arctic. The occurrence of

C. quadridentata var. *arctica* on Victoria Island is the only record of this genus in the arctic islands, which suggests that the family is not well adapted to high arctic and polar desert environments.

Quantitative Results between Sites[1]

Total number of acarine species and number of species of Oribatei, Prostigmata and Mesostigmata at each of the 34 sites is superimposed on a map of northern North America (Figure 2). There is a decrease in number of species with increasing latitude. Causes include, the shorter post-glacial period, increasing climatic harshness and decreasing food resources for the mites, associated with reduced vegetation. Exceptions to this are Baffin Island and Ellesmere Island.

The climate of the southern part of Baffin Island is milder than that of other islands in the arctic archipelago. Subarctic conditions exist in the extreme south of the island, although parts of the north are still glaciated. Baffin Island is also situated in proximity to Greenland.

Ellesmere Island may have partially been an ice-free refugium during the last glaciation (Blake, 1970). Brassard (1971) found 151 species of moss in northern Ellesmere Island, 50 per cent of which are rare.

Ratio of Oribatei to Prostigmata

Douce (1973) working at Point Barrow was the first to demonstrate the importance of Prostigmata at a high arctic site. In the present study, the majority of high arctic and polar desert localities, such as Bathurst Island, King Christian Island, Seymour Island, Somerset Island, northern Ellesmere Island, Devon Island and Igloolik Island show greater diversity of Prostigmata than of other acarine groups (Figure 3). Axel Heiberg Island and North Kent Island are exceptions possibly because of the small number of samples taken at these sites. In mid to low arctic and subarctic habitats Oribatei are more diverse than Prostigmata (Figure 3).

Ratio of Acari to Collembola

The ratio of numbers of individual mites to Collembola in soil faunal studies is generally positive (Forsslund, 1945; Murphy, 1953; Behan et al., 1978). In the present study, mite

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[1] These results are based on raw data because of variability in a) sampling methods, size of samples, sampling personnel and time between sample collection and extraction; b) types of habitats sampled at each site. As a result only minimal statistical analysis could be carried out.

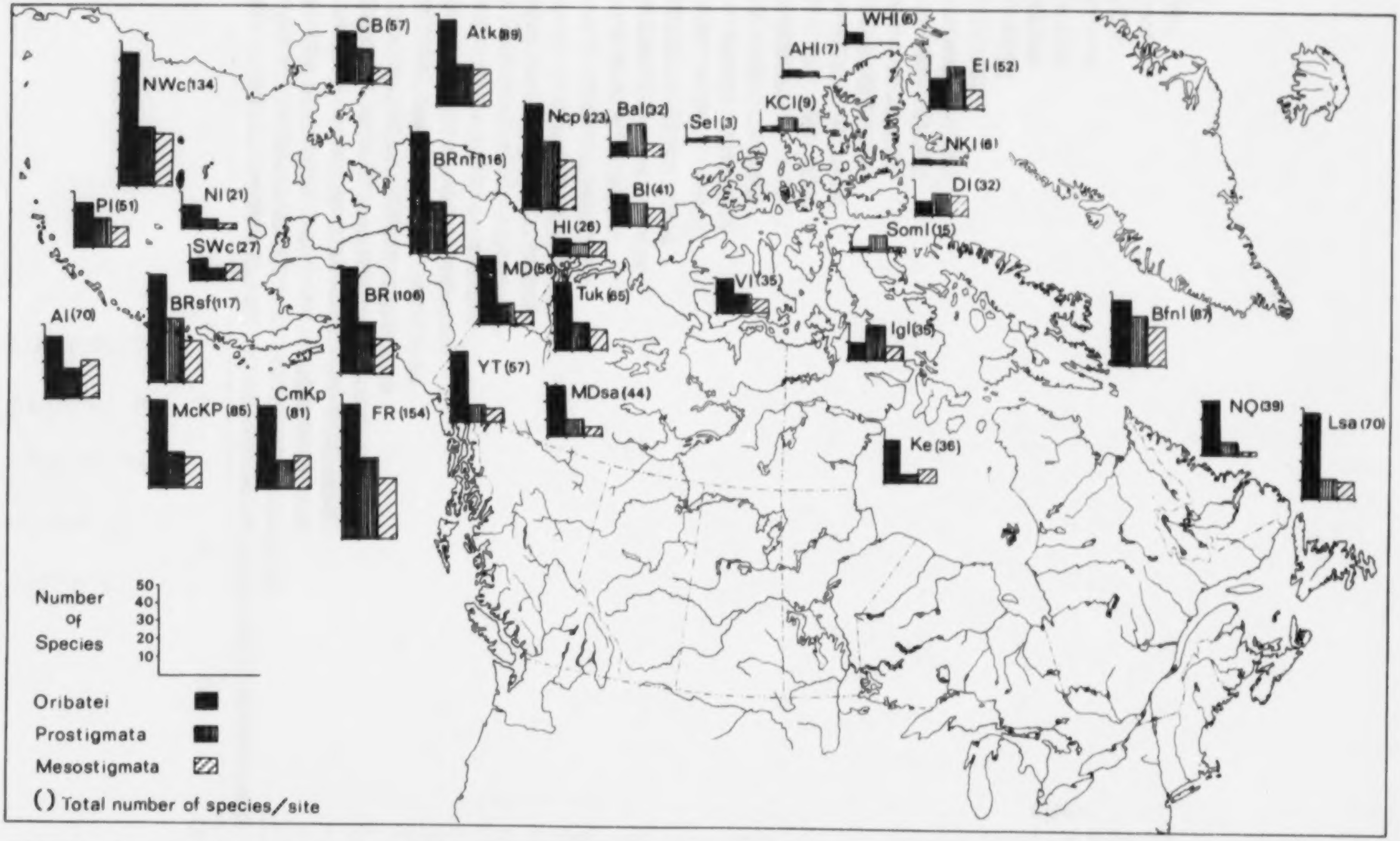
CB(57)
Atk(89)
NWc(134)
PI(51)
NI(21)
SWc(27)
AI(70)
BRsf(117)
BRnf(116)
BR(106)
McKP(85)
CmKp (81)
FR(154)
YT(57)
MD(56)
Tuk(65)
MDsa(44)
HI(26)
Ncp(123)
Bal(32)
BI(41)
Sel(3)
KCI(9)
AHI(7)
WHI(6)
EI(52)
NKI(6)
DI(32)
SomI(15)
VI(35)
IgI(35)
Ke(36)
Bfnl(87)
NQ(39)
Lsa(70)
Number of Species
50
40
30
20
10
Oribatei
Prostigmata
Mesostigmata
() Total number of species/site

FIGURE 2. Total number of acarine species and the number of species of Oribatei, Prostigmata and Mesostigmata at 35 sites in the North American arctic and subarctic, and northern Chukotka, U.S.S.R.[1]

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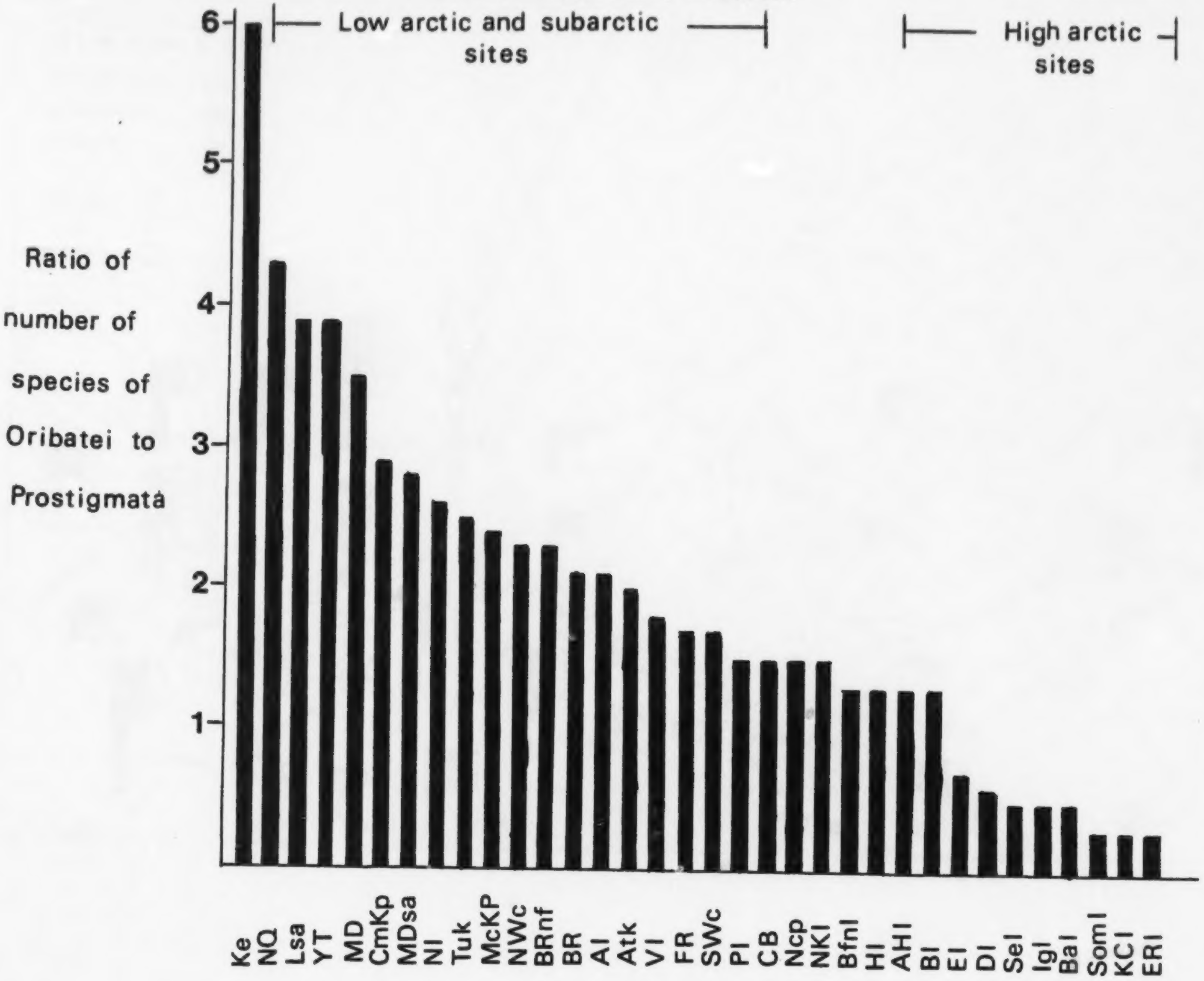
[1] Abbreviations as in Table 1.

FIGURE 3. Ratio between number of species of Oribatei and Prostigmata for sites in the North American arctic and subarctic and northern Chukotka, U.S.S.R.[1]



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[1] Abbreviations as in Table 1.

to Collembola ratios are available for 16 sites (Figure 4). Although results are not statistically significant, the ratio tends to be lowest in mid to high arctic and polar desert localities. Bathurst, Devon, Igloolik and North Kent Islands, for example, have a ratio of less than or approximately one. Previous studies from arctic localities support these results (Douce, 1973; Watson et al., 1966).

Community Analysis Between Sites

Sørensen's quotient of similarity (Sørensen, 1948) was used to determine affinities between arctic and subarctic sites on the basis of the mite fauna of each site. Species lists from 36 sites were analysed, 34 from the present study and data from Ellef Rignes Island (McAlpine, 1965) and Melville Island (Lindquist, in lit., 1977). Where species other than those recorded in the present study are known to occur at a particular site, they were included in this analysis. Indices of similarity for the 36 sites are given (Table 3), sites having a high similarity being adjacent.

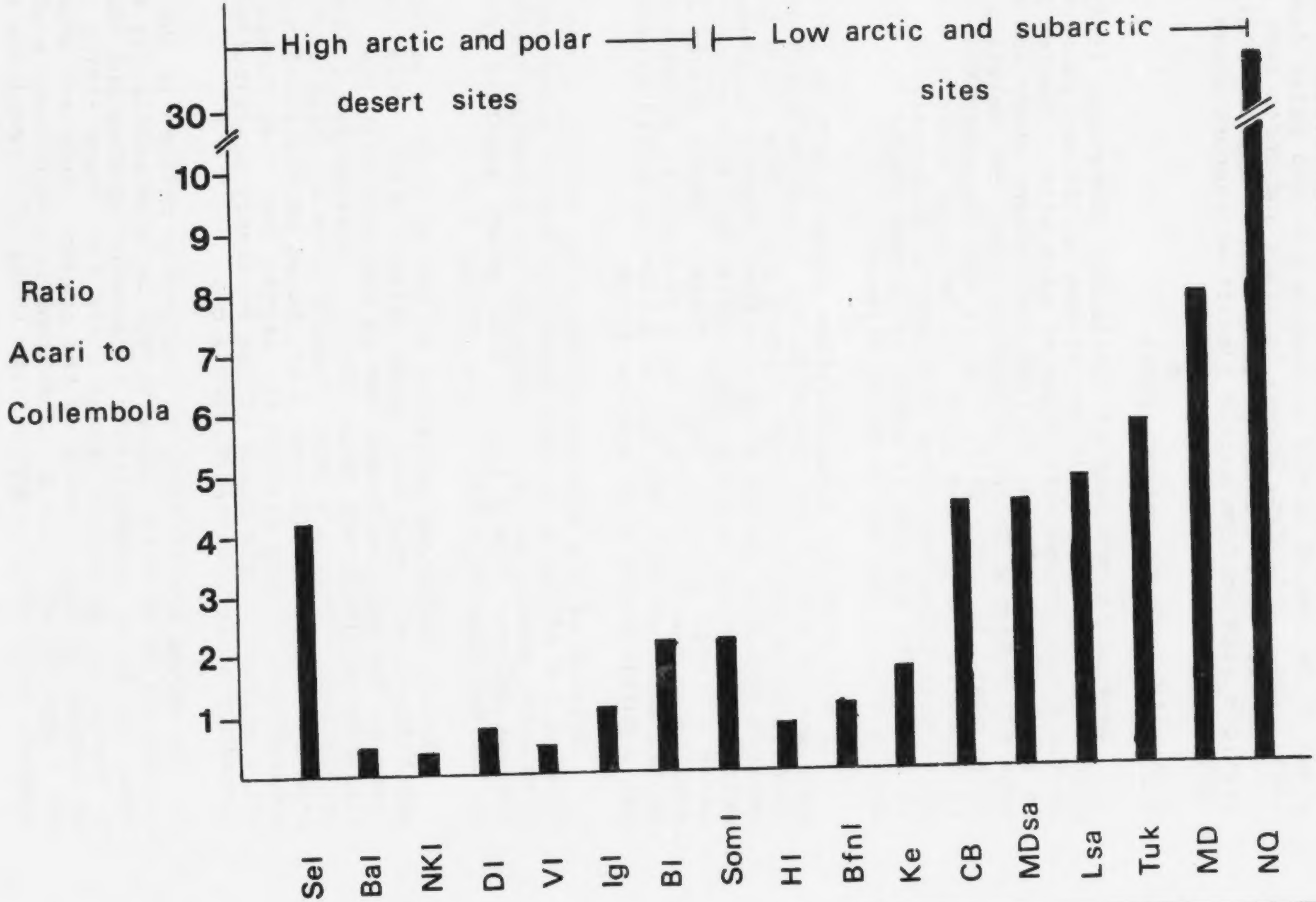
A hierarchical classification using data from Sørensen's quotient of similarity (Table 3) was developed based on the formula of Mountford (1962) (Figure 5). This shows that western Canadian arctic sites are most similar to Alaskan sites, which is expected based on the Pleistocene history of the western arctic (Hultén, 1968). These combined groups are more similar to the Soviet arctic than they are to islands in the arctic archipelago. The one exception is Baffin Island, which has a particularly rich acarine fauna.

Islands of the extreme northwestern arctic, although showing low affinity to each other, do form a group separate from other arctic sites. Similarly, the Aleutian, Pribilof and Nunivak Islands form a loosely knit group, separate from other arctic and subarctic localities (Figure 5).

Groups delimited in Figure 5 can be used to divide the North American arctic into zones (Figure 6 a). This zonation, based on the acarine fauna, can be compared with that of Alexandrova (1970) and Young (1971). Alexandrova divided the arctic into: Zone 1 - polar desert; Zone 2 - high arctic; Zone 3 - low arctic (Figure 6 b), based on the floristic composition. Young divided the arctic into four floristic zones defined on the basis of the northerly distribution of certain vascular plants (Figure 6 c).

As mites are directly or indirectly related to the vegetation in an area, there should be some similarity between zonations based on similarity of acarine species and those based on vegetation patterns. Zones 1 and 4 of Young (1971) correspond to Zone A and C of the present study and Zone 2 and 3 approximate Zone B. Zonations in the present study, however, most closely approximate those of Alexandrova (1970).

FIGURE 4. Ratio between the number of individual mites and Collembola at 17 sites in the North American arctic and subarctic and northern Chukotka, U.S.S.R.[1]



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[1] Abbreviations as in Table 1.

FIGURE 5. Hierarchical classification of 37 sites in the North American arctic and subarctic and northern Chukotka, U.S.S.R., based on Sørensen's index of similarity.

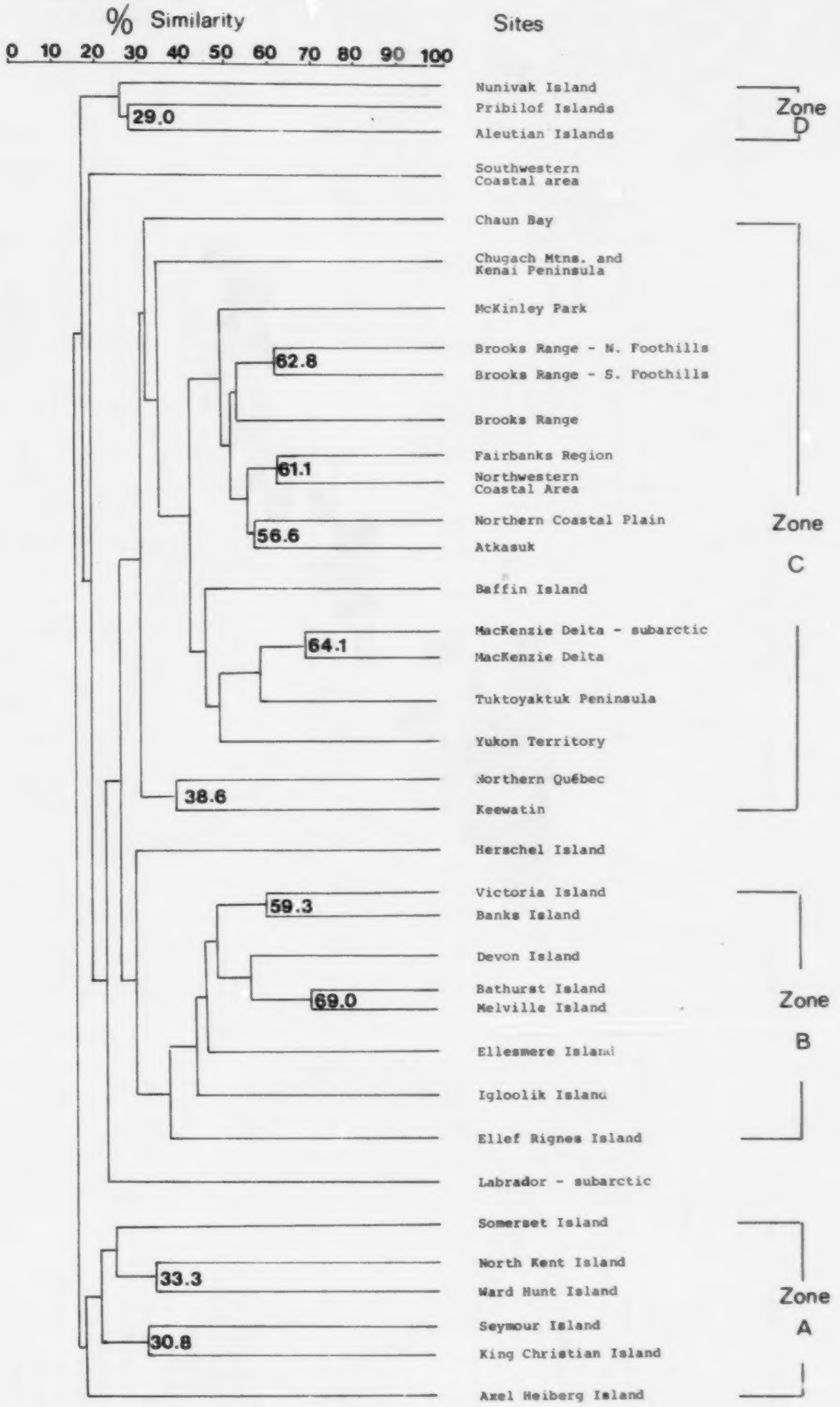
% Similarity
0 10 20 30 40 50 60 70 80 90 100
Sites
Nunivak Island
Pribilof Islands
Aleutian Islands
29.0
Zone D
Southwestern Coastal area
Chaun Bay
Chugach Mtns. and Kenai Peninsula
McKinley Park
Brooks Range - N. Foothills
Brooks Range - S. Foothills
62.8
Brooks Range
Fairbanks Region
Northwestern Coastal Area
61.1
Northern Coastal Plain
Atkasuk
56.6
Zone C
Baffin Island
MacKenzie Delta - subarctic
MacKenzie Delta
64.1
Tuktoyaktuk Peninsula
Yukon Territory
Northern Québec
Keewatin
38.6
Herschel Island
Victoria Island
Banks Island
59.3
Devon Island
Bathurst Island
Melville Island
69.0
Zone B
Ellesmere Island
Igloolik Island
Ellef Rignes Island
Labrador - subarctic
Somerset Island
North Kent Island
Ward Hunt Island
33.3
Zone A
Seymour Island
King Christian Island
30.8
Axel Heiberg Island

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Table 3. Sørensen's index of similarity for 37 sites in the North American arctic and subarctic and northern Chukotka, U.S.S.R.

SITES[1]	NI	PI	AI	SWc	CB	CaMp	Ncp	BRnf	NWc	FR	Atk	BR	McKP	BRsf	MDsa	MD	TuP	YT	BfnI	BI	MI	BaI	DI	EI	VI	IgI	ERI	NQ	Lsa	K	HI	SomI	NKI	WHI	SeI	KCI	AHI
NUNIVAK ISLAND																																					
PRIBILOF ISLANDS	27.8																																				
ALEUTIAN ISLANDS	26.4	29.8																																			
SOUTHWESTERN COASTAL AREA	20.8	20.5	14.4																																		
CHAUN BAY	15.4	20.4	17.3	26.2																																	
CHUGACH MTNS. & KENAI P.	17.7	28.8	33.1	22.2	17.4																																
NORTHERN COASTAL PLAIN	12.5	27.6	22.8	22.7	35.6	31.4		■	■	■	■	■	■	■	■	■																					
BROOKS RANGE - N. FOOTHILLS	18.9	34.4	29.6	30.1	31.9	40.6	55.0		■	■	■	■	■	■	■	■				GROUP 1												■	QS > 45%				
NORTHWESTERN COASTAL AREA	20.7	31.4	29.4	28.6	37.7	43.7	58.4	56.7		■	■	■	■	■																							
FAIRBANKS REGION	11.4	20.5	25.9	23.2	31.3	41.7	54.2	54.6	61.1		■	■	■	■	■																						
ATKASUK	18.2	30.0	22.6	27.6	39.7	32.9	56.6	55.5	57.4	49.4		■	■			■																					
BROOKS RANGE	14.2	25.5	26.1	28.6	28.2	37.4	55.9	55.7	57.5	49.2	65.1			■		■																					
MCKINLEY PARK	17.0	25.0	34.8	21.4	35.2	44.6	47.1	54.5	50.2	53.6	50.6	42.9		■																							
BROOKS RANGE - S. FOOTHILLS	13.0	25.0	25.7	26.4	26.4	37.4	45.0	62.8	50.2	50.2	43.7	48.4	46.5																								
MACKENZIE DELTA - SUBARCTIC	13.6	21.0	16.8	14.5	31.0	26.0	46.2	51.6	39.5	45.3	39.5	43.3	36.7	39.5		■	■	■	■				GROUP 2														
MACKENZIE DELTA	25.3	24.0	19.4	21.8	33.6	33.6	45.7	50.0	40.8	44.7	55.2	45.6	44.0	40.8	64.1		■	■	■																		
TUKTOYAKTUK PENINSULA	14.0	29.3	19.3	13.0	26.2	30.1	42.6	44.4	34.1	39.3	44.7	40.9	36.0	34.1	47.2	56.3		■		■																	
YUKON TERRITORY	10.3	16.7	17.3	19.1	31.6	27.5	34.4	36.8	37.9	37.0	39.7	39.3	33.8	37.9	47.7	52.2	45.3																				
BAFFIN ISLAND	9.3	17.4	15.3	12.3	26.4	19.1	40.0	37.3	32.4	34.9	40.9	34.2	29.1	32.4	52.0	45.6	44.7	38.4		■				■							GROUP 3						
BANKS ISLAND	6.5	21.7	18.0	11.8	22.5	19.7	36.6	36.7	29.1	25.6	30.8	28.6	31.8	29.1	38.2	40.3	49.6	37.4	50.4		■	■	■	■	■	■											
MELVILLE ISLAND	12.8	26.0	10.4	15.1	16.9	15.0	37.2	31.8	21.0	15.6	26.1	28.8	19.8	21.0	29.2	34.0	37.4	29.1	40.7	56.7		■	■	■	■	■	■										
BATHURST ISLAND	7.6	19.3	11.8	10.2	18.0	12.4	23.2	24.6	16.1	16.1	19.8	20.3	17.1	16.1	25.0	22.6	22.0	23.4	25.4	45.6	69.0		■	■			■										
DEVON ISLAND	3.8	19.3	11.8	6.8	9.0	12.4	23.2	20.3	13.4	12.9	16.5	17.4	15.4	13.4	22.1	22.4	30.4	25.6	31.0	50.7	55.2	55.2			■												
ELLESMERE ISLAND	5.1	20.2	14.1	14.1	20.9	14.4	33.2	32.9	24.0	20.8	24.5	26.8	25.2	24.0	35.5	27.3	32.5	24.4	45.5	48.5	57.1	46.7	37.8														
VICTORIA ISLAND	21.4	30.2	17.1	16.1	28.3	19.0	31.7	39.7	26.3	20.1	30.7	25.5	30.0	26.3	32.9	38.9	35.3	33.3	38.3	59.3	45.9	38.2	46.7	32.6													
IGLOOLIK ISLAND	10.7	23.3	22.9	16.1	19.6	18.8	31.7	32.0	21.1	20.1	25.8	25.5	26.7	21.1	25.9	29.4	35.0	24.7	39.7	51.2	52.5	34.8	39.3	38.7	36.6												
ELLEF RINGNES ISLAND	0.0	9.4	7.2	10.0	8.6	4.3	14.7	15.1	10.8	7.2	13.7	11.8	10.2	10.8	13.0	11.8	15.2	13.7	16.5	34.5	46.2	48.9	43.2	28.2	25.5	29.2											
NORTHERN QUEBEC	6.7	15.6	12.8	12.1	29.2	18.3	25.9	29.0	20.5	23.8	31.3	20.9	21.0	20.5	36.8	42.1	37.0	31.4	31.7	29.9	21.5	16.2	21.2	24.7	34.2	13.0	7.5										
LABRADOR - SUBARCTIC	4.8	13.2	12.9	10.3	15.8	15.9	18.7	33.0	25.7	25.0	22.6	15.9	23.2	25.7	33.0	29.2	30.4	30.3	26.9	17.1	18.8	13.5	10.4	23.4	15.1	15.0	2.4	33.3									
KEEWATIN	10.5	18.4	15.1	19.1	23.7	23.9	28.9	36.6	30.1	24.2	28.8	31.0	24.8	30.1	39.2	36.8	44.0	35.0	37.8	43.2	38.7	29.3	29.9	25.5	39.0	33.3	18.5	38.6	23.0								
HERSCHEL ISLAND	17.0	20.8	16.7	28.4	21.7	13.1	30.9	28.8	23.8	23.3	27.8	28.8	28.8	23.8	31.2	35.0	37.1	28.6	34.8	34.2	30.8	28.6	29.1	28.6	43.1	18.2	23.8	19.7	17.8	30.6							
SOMERSET ISLAND	5.3	8.8	11.5	13.6	16.2	6.1	15.7	9.0	9.3	12.9	9.4	7.5	11.8	7.5	14.3	11.4	19.5	10.5	24.0	32.8	18.6	25.0	30.0	26.7	24.0	27.5	14.8	10.7	11.6	14.0	31.1						
NORTH KENT ISLAND	7.4	3.5	5.3	0.0	6.4	4.6	4.7	5.4	7.1	6.3	4.2	0.0	8.8	3.3	6.8	10.1	11.0	3.0	11.0	11.5	6.3	15.4	6.5	12.5	9.8	14.3	22.2	4.3	2.6	4.2	16.7	28.6					
WARD HUNT ISLAND	0.0	6.9	2.6	5.9	9.4	4.6	4.6	7.1	2.8	5.0	4.2	5.3	4.4	3.2	8.5	7.6	12.0	6.0	8.8	11.5	5.6	10.3	12.9	9.2	14.6	9.5	11.1	4.3	5.2	12.5	11.1	19.0	33.3				
SEYMOUR ISLAND	0.0	0.0	0.0	6.7	6.7	2.4	3.2	3.7	1.5	2.6	4.4	3.7	2.3	1.7	5.3	5.3	5.7	6.3	6.8	8.2	20.7	16.7	14.3	6.6	10.5	15.4	40.0	0.0	2.7	4.4	6.1	22.2	22.2	22.2			
KING CHRISTIAN ISLAND	0.0	6.7	5.1	5.6	12.1	4.4	9.1	7.0	4.7	6.1	6.1	7.7	8.5	4.8	11.6	16.5	13.0	14.1	14.7	25.0	34.3	32.6	34.3	17.9	22.2	17.4	36.4	11.8	9.9	11.5	25.0	28.6	25.0	33.3	22.2		
AXEL HEIBERG ISLAND	14.3	10.3	7.8	11.8	3.1	11.4	10.8	10.6	8.5	6.2	8.3	10.6	8.7	8.1	6.8	0.0	8.1	11.8	13.0	22.6	36.4	25.0	25.0	15.4	33.3	27.9	21.1	4.2	2.6	16.3	16.2	27.3	15.4	15.4	20.0	11.8	

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[1] Abbreviations as in Table VII.

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Inconsistencies between the two zonations are:

a) Inclusion of the northern half of Ellesmere Island in Zone 1 (Figure 6 b). Based on both the acarine fauna and vegetation analysis (Brassard, 1971), this area should be included in Zone 2.

b) Somerset Island is included in Zone A (Figure 6 a). Samples from this site were, however, from a restricted coastal area. Further study of this site may alter the present data on acarine diversity.

c) The lower limit of Zone 3 (Alexandrova, 1970) and Zone 4 (Young, 1971) is treeline. No such definite boundary is evident in zonations based on the mite fauna (Figure 6 a). Although, in the present study, species are found in subarctic and not in arctic localities, there is generally a closer similarity between arctic and subarctic sites in the same geographical location than between arctic sites in general. Treeline, therefore, apparently has little affect on soil mites, except the macrophytophagous Phthiracaroidea, which are common in coniferous litter and rare in the arctic.

All of the Acari in Zone A have a circumpolar distribution similar to the plant species (Young, 1971). They tend to be species of common occurrence in a wide variety of habitats throughout arctic regions. In Zones B and C the percentage of circumpolar species decreases rapidly.

GENERAL DISCUSSION AND CONCLUSIONS

The survey of changes in diversity and density of arctic soil Acari, recorded in this study, with changes in latitude, is summarized in Table 4. In subarctic localities, as in most temperate areas, Oribatei are the dominant component of the soil Acari. Oribatid dominance continues into low arctic sites, but, as the environment becomes increasingly harsh, there is a rapid drop in oribatid diversity and Prostigmata take over as the dominant group. The overall decrease in mite diversity by a factor of seven from subarctic to polar desert is correlated with increasing severity of abiotic factors and decreasing annual primary productivity.

The four-fold decrease in both oribatid and mesostigmatid diversity from low to high arctic is more marked than the decrease from either subarctic to low arctic or high arctic to polar desert. In the present study high arctic sites are all insular, as Point Barrow, a high arctic site (Douce and Crossley, 1977) was not considered separately from northern coastal arctic. If species that occur at Point Barrow are included in the high arctic

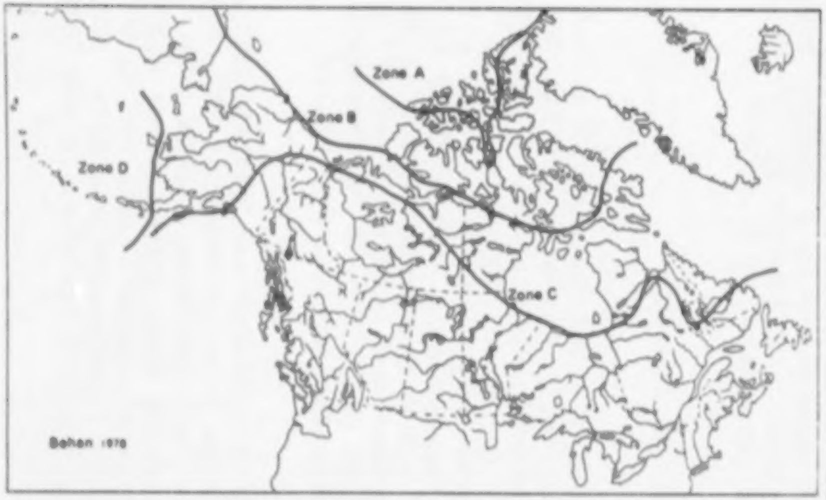

Zone A
Zone B
Zone C
Zone D
Behan 1970

FIGURE 6 a. Zonation of the North American arctic on the basis of the soil Acari.

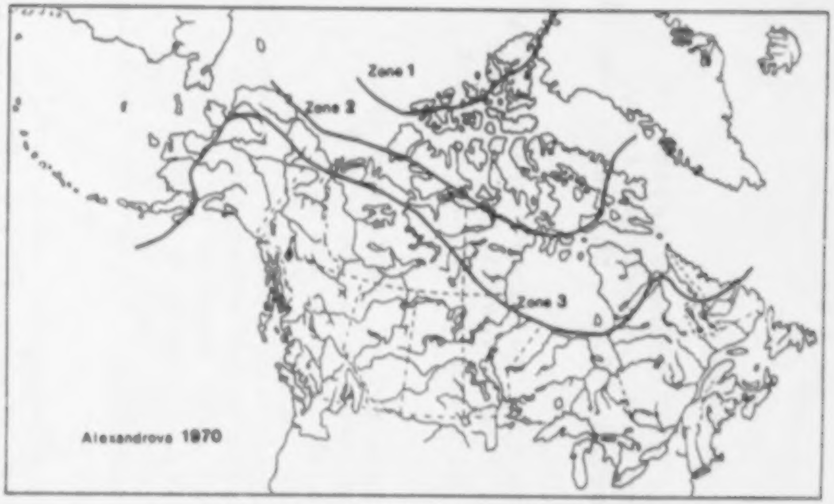

Zone 1
Zone 2
Zone 3
Alexandrova 1970

FIGURE 6 b. Zonation of the North American arctic on the basis of its vegetation (Alexandrova, 1970).

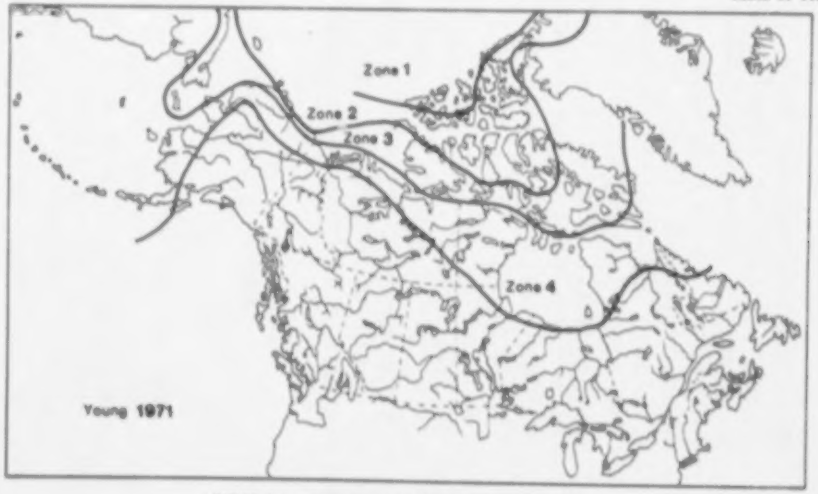
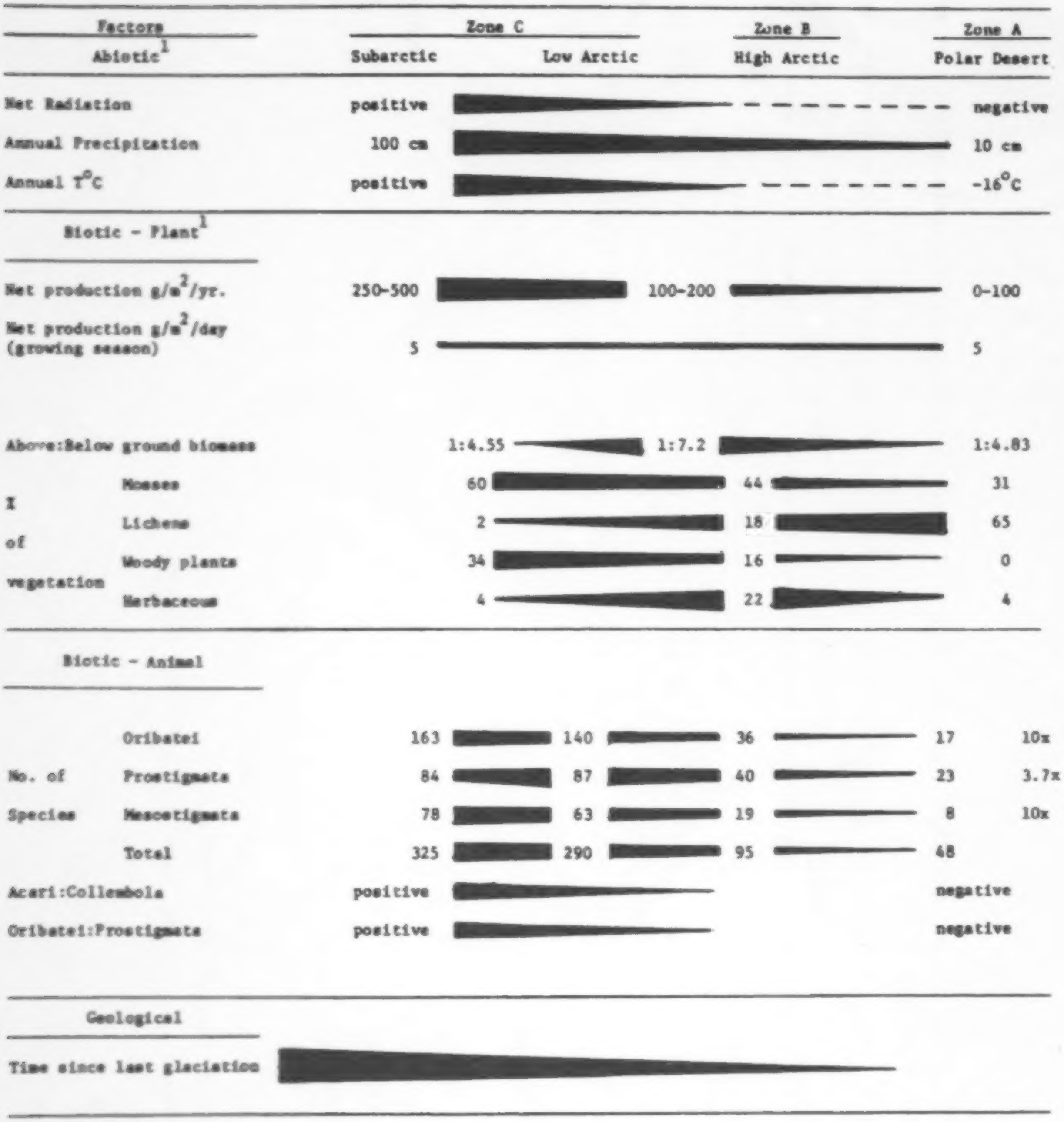

Zone 1
Zone 2
Zone 3
Zone 4
Young 1971

FIGURE 6 c. Zonation of the North American arctic on the basis of floristics (Young, 1971).

TABLE 4. Summary of changes in abiotic and biotic factors with latitude from subarctic to polar desert.



Factors		Zone C		Zone B	Zone A	
Abiotic[1]		Subarctic	Low Arctic	High Arctic	Polar Desert	
Net Radiation		positive			negative	
Annual Precipitation		100 cm			10 cm	
Annual T°C		positive			-16°C	
Biotic - Plant[1]						
Net production g/m²/yr.		250-500		100-200	0-100	
Net production g/m²/day (growing season)		5			5	
Above:Below ground biomass			1:4.55	1:7.2	1:4.83	
% of vegetation	Mosses		60	44	31	
	Lichens		2	18	65	
	Woody plants		34	16	0	
	Herbaceous		4	22	4	
Biotic - Animal						
No. of Species	Oribatei	163	140	36	17	10x
	Prostigmata	84	87	40	23	3.7x
	Mesostigmata	78	63	19	8	10x
	Total	325	290	95	48	
Acari:Collembola		positive			negative	
Oribatei:Prostigmata		positive			negative	
Geological						
Time since last glaciation						

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[1] From Webber (1974).

TABLE 5. Changes in density and diversity of arctic soil Acari with latitude from subarctic to polar desert.

Acari	Zone C		Zone B		Zone A
	Subarctic	Low Arctic	High Arctic		Polar Desert
Number of Species			With Point Barrow[3]	Without Point Barrow[2]	
Oribatei	163 (9.6)[1]	140 (8.2)	48 (2.8)	36 (2.1)	17 (1)
Prostigmata	84 (3.7)	87 (3.8)	54 (2.3)	40 (1.7)	23 (1)
Mesostigmata	78 (9.8)	63 (7.9)	26 (3.3)	19 (2.4)	8 (1)
Total Acari	325 (6.8)	290 (6.0)	128 (2.7)	95 (2.0)	48 (1)
Ratios					
Prostigmata:Mesostigmata	1.1:1	1.4:1	2.1:1	2.1:1	2.9:1
Oribatei:Mesostigmata	2.1:1	2.2:1	1.8:1	1.9:1	2.1:1
Oribatei:Prostigmata	1.9:1	1.6:1	0.9:1	0.9:1	0.7:1

[1] Diversity expressed as a ratio of polar desert diversity.

[2] High arctic sites that are all insular.

[3] High arctic areas including the mainland site, Point Barrow, Alaska.

data, a more gradual decrease in diversity from low to high arctic is evident (Table 5). This suggests that some of the four-fold decrease in diversity is a result of difficulties in dispersal from mainland to island sites.

While there is a ten-fold decrease in oribatid and mesostigmatid diversity between subarctic and polar desert, there is only a four-fold decrease in Prostigmata. On the basis of what is presently known of Prostigmata survival capacity, tolerance of low relative humidity, shorter life-span and greater egg-laying capacity than that of Oribatei, they can be considered r-strategists and can probably invade more arid environments than Oribatei (Atyeo, 1960; Jeppson, Keifer and Baker, 1975; Douce and Crossley, 1977).

If the dimension of geological time is included in the gradient from subarctic to polar desert, there is the added factor of decreasing years since glacial retreat. Polar desert sites can, therefore, be considered as youthful seral stages in the tundra biome (McAlpine, 1964; Dunbar, 1968). In such areas, successful species tend to have the biological characteristics of Prostigmata (Margalef, 1975). In the Antarctic,Prostigmata are also the dominant acarine group and are represented by the same families as in arctic polar desert: Nanorchestidae, Eupodidae and Rhagidiidae (Janetschek, 1967).

The ratio of population density of Acari to Collembola decreases in general along the latitudinal gradient from subarctic to polar desert. In the Alps, Janetschek (1949, 1958) demonstrated that in the first stage of recolonization after the glacial tongue has withdrawn, Collembola are predominant. He observed that as the habitat matured and its soil and vegetation developed, Collembola decreased in density relative to mites. Collembola are also numerically dominant in all habitats in the antarctic (Janetschek, 1967, 1970). This overall predominance in cold desert localities is probably related to their short life-span and high intrinsic rate of increase (Douce and Crossley, 1977).

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ASPECTS OF THE ECOLOGY OF ANTARCTIC SOIL FAUNA

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INTRODUCTION

The Antarctic Region can be divided into ecological zones (Holdgate, 1964) including the sub-Antarctic, the maritime and continental zones. This paper is concerned with the maritime Antarctic zone south of 60° latitude. The majority of land habitats seasonally free of snow and ice occur here and hence its importance to the soil fauna. It is also an area in which much of the Antarctic soil biological work has been undertaken. The maritime Antarctic zone south of 60° latitude includes the South Orkney and South Shetland Islands, together with Adelaide Island and the west coast of the Antarctic (Graham Land) Peninsula and its offshore islands.

Apart from the microbial groups (fungi, yeasts and bacteria) in maritime Antarctic soils, there are eight invertebrate groups represented ranging from Protozoa to higher insects (Diptera). Table 1 presents the numbers of species found to date for these groups. Due to their wide distribution throughout the maritime Antarctic and the increasing body of information about them, this paper will concentrate on the arthropods in general and on the mites (Acari) and springtails (Collembola) in particular. Such soil micro-arthropods penetrate further south than most other invertebrates, and exhibit ecological features and adaptations to the environment, which may be considered typical of the Antarctic soil fauna generally. The soil fauna is the dominant terrestrial component, there being no permanent land dwelling vertebrates and above ground invertebrates are generally absent. There is considerable variation of terrestrial habitats within the maritime Antarctic, and Holdgate (1977) has discussed this in detail. Briefly, invertebrate soil communities are found in a range of habitats from exposed fellfield types (similar to the chalikosystem of Janetschek, 1967) to the closed moss dominated (bryosystem) in addition to relatively small areas covered by flowering plants (the grass Deschampsia antarctica Desv. and the cushion plant Colobanthus crassifolius (D'Urv.) Hook.f. Much of the information reviewed here has been collected from bryophyte communities on Signy Island in the South Orkney Islands, where arthropods occur in relatively large numbers and the fauna is comparatively diverse. Two sites have been investigated in detail: SIRS (Signy Island Reference Site) 1 and SIRS 2. The former is a fairly dry moss turf composed of Polytrichum alpestre Hoppe and Chorisodontium aciphyllum (Hook.f. et Wils.) Broth., whilst the latter is a relatively wet moss carpet composed of Calliergon sarmentosum (Wahlenb.) Kindb., Calliergidium austro-stramineum (C. Muell.) Bartr. and Drepanocladus uncinatus (Hedw.) Warnst.

TABLE 1

SOIL INVERTEBRATES OF MARITIME ANTARCTIC HABITATS

	No. of species recorded		Distribution	Reference
Protozoa	124		Ubiquitous	Smith, 1978
Rotifera	Number unknown but Adineta, other Bdelloidea, and Monogononta recorded		Mainly in wet moss communities	Jennings, 1976 a
Tardigrada	11		Wet moss communities	Jennings, 1976 b
Nematoda	40		Ubiquitous	Maslen, in press
Enchytraeidae	2 ?		Organic detritus in South Shetland Islands	Block, unpublished
Collembola	8		Ubiquitous	Wise, 1967; Wallwork, 1973
Diptera	2		South Shetland Islands, Antarctic Peninsula	Wirth & Gressitt, 1967
Acari	40		Ubiquitous	Gressitt, 1967; Wallwork, 1973
	Mesostigmata	9		
	Cryptostigmata	16		
	Astigmata	5		
	Prostigmata	10		

This review will consider aspects of the ecology and physiology of micro-arthropods living in these communities, which highlight their adaptations to the environment of the maritime Antarctic. These include features of their populations, life cycles, respiratory metabolism and cold tolerance.

ECOLOGY

Species composition

Consideration of the arthropod species list (Table 2) for the two moss sites at Signy Island shows a typical structure with the majority of the fauna comprised of prostigmatid mites, three collembolans, two cryptostigmatids and a single mesostigmatid predator. In general, a species poor and much simplified arthropod community than that found in temperate habitats.

Population density

The most numerous species present on the SIRS (Table 3) is the ubiquitous springtail *Cryptopygus antarcticus* Willem, which over a two year study period maintained a mean population of 48,296 individuals m^{-2}, six times as many as all the Acari. The Acari averaged *c*. 8,223 individuals m^{-2} for the same period. Between year differences occurred in two species of Prostigmata, *Nanorchestes antarcticus* (Strandtmann) and *Ereynetes macquariensis* (Fain), which showed over 50% decline in numbers during the second year. *Eupodes minutus* (Strandtmann) and *Gamasellus racovitzai* (Trouessart) maintained fairly constant numbers for 1972 and 1973.

Seasonal changes in mite population density were recorded (Figure 1, from Goddard, 1979) which followed a pattern of low numbers in winter with high summer numbers. *G. racovitzai* was the only species which had similar yearly cycles of abundance, which may be related to its predatory role in the community. Few seasonally related changes occurred in the collembolan population of this site (Tilbrook, 1977).

In terms of vertical distribution, most Acari and Collembola were found in the uppermost layer of the moss peat profile, except during winter when a reversal of the proportion of the total mite population in the 0-3 cm and 3-6 cm layers occurred. *N. antarcticus* was consistently (80-90% of its population) in the 0-3 cm stratum throughout the year, whilst *E. macquariensis* was found mainly at 3-6 cm. Deeper core samples collected on four occasions (Figure 2) revealed that Acari did not penetrate beyond 18 cm in the profile, and confirmed that *E. macquariensis* was a deeper dwelling form than the other species present. Little information exists on the horizontal distribution of the micro-arthropods on these sites, but they appear to be highly aggregated especially during spring and the early part of the austral summer.

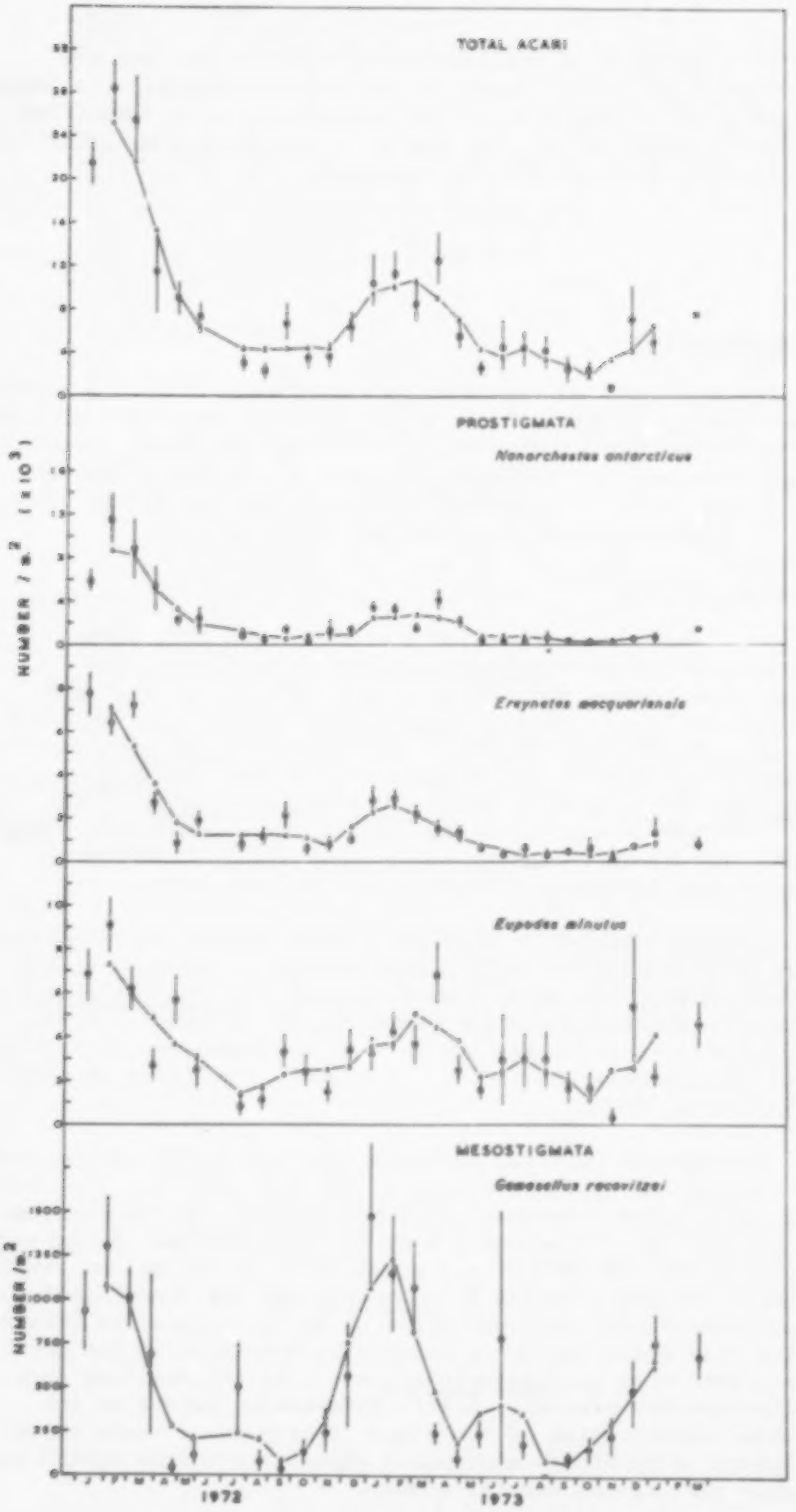

FIGURE 1. Seasonal fluctuations in mean population density ($x10^3$ ind m^{-2}) on SIRS 1 during 1972-74. Monthly mean values (±SEM) are plotted from Goddard, 1979.

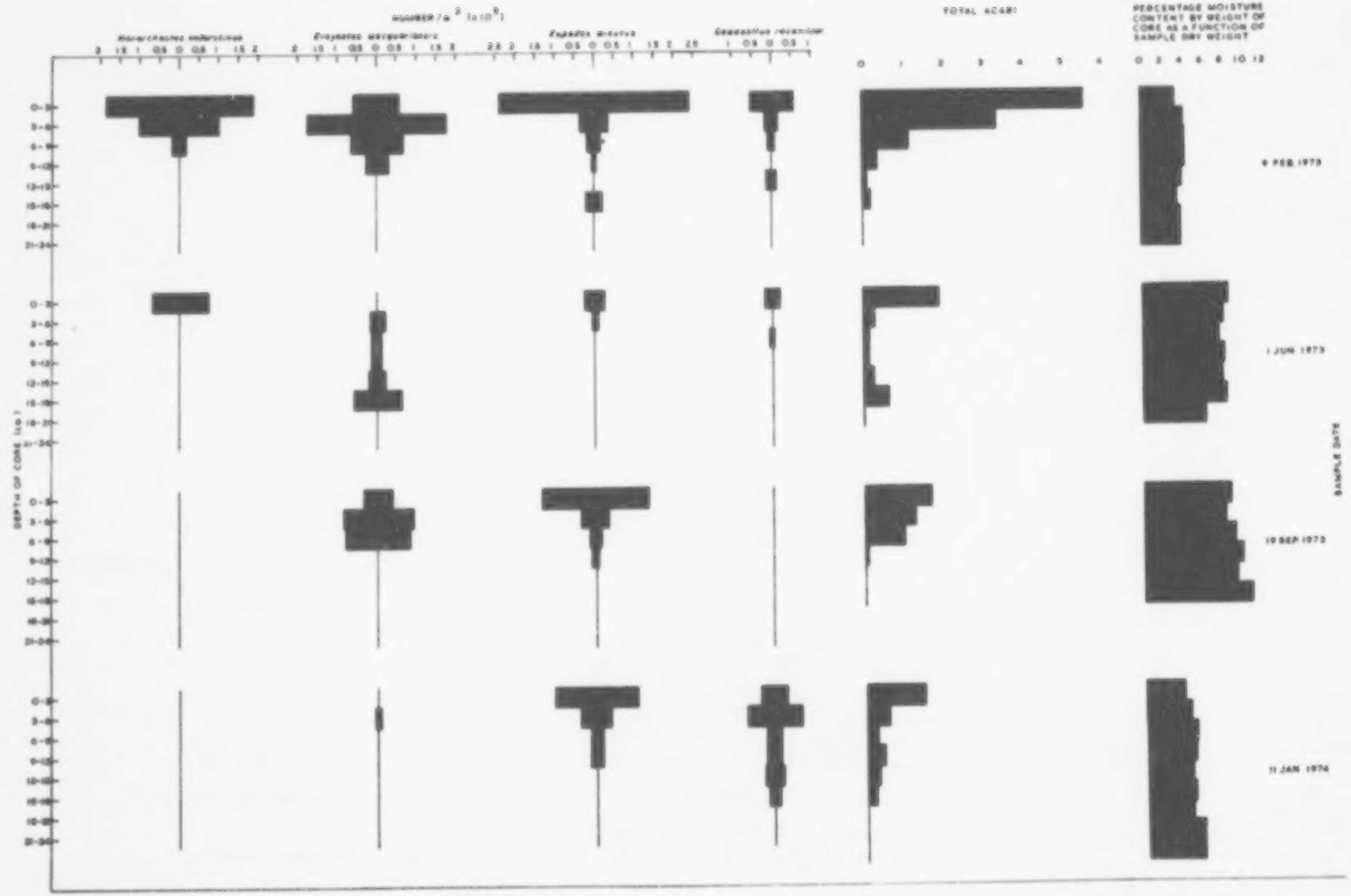

FIGURE 2. Vertical distribution of Acari in 24 cm deep cores on SIRS 1 (two winter and two summer samples) together with water content as percentage of core dry weight.

TABLE 2

SPECIES OF ACARI AND COLLEMBOLA RECORDED FOR TWO MOSS SITES AT SIGNY ISLAND, MARITIME ANTARCTIC

ACARI			
	Cryptostigmata	2 species	*Alaskozetes antarcticus* (Michael) *Halozetes belgicae* (Michael)
	Mesostigmata	1 species	*Gamasellus racovitzai* (Trouessart)
	Prostigmata	6 species	*Nanorchestes antarcticus* (Strandtmann) *Eupodes minutus* (Strandtmann) *Halotydeus signiensis* (Strandtmann) *Ereynetes macquariensis* (Fain) *Stereotydeus villosus* (Trouessart) *Tydeus tilbrooki* (Strandtmann)
	Astigmata	1 species	*Neocalvolia antarctica* (Hughes & Tilbrook)
COLLEMBOLA			
		3 species	*Cryptopygus antarcticus* Willem *Frisea grisea* (Schaffer) *Parisotoma octooculata* (Willem)

TABLE 3

ANNUAL MEAN POPULATION DENSITIES FOR FOUR COMMON SPECIES OF ACARI AND COLLEMBOLA FOUND IN THE SIRS 1 SAMPLES

Numbers of individuals m^{-2}

Year	Nanorchestes antarcticus	Ereynetes macquariensis	Eupodes minutus	Gamasellus racovitzai	Total Acari	Total Collembola*
1972	3,376	2,752	3,877	464	10,469	60,410
1973	1,278	1,086	3,144	469	5,977	36,182
1972 and 1973	2,327	1,919	3,510	467	8,223	48,296

* Entirely Cryptopygus antarcticus

Population biomass

Total acarine biomass varied from 23.0 to 38.2 mg live m^{-2} for the two year study. Of this *G. racovitzai* contributed 44 and 57% respectively, the remainder being made up of the three prostigmate species. Following the decline in population density, the live weight mite biomass decreased by *c.* 40% from 1972 to 1973 (Figure 3).

For *C. antarcticus*, live weight biomass varied from 432.5 to 1,124.8 mg m^{-2} during 1972, with an annual mean of 793.4 mg m^{-2}, which was 26 times greater than the Acari.

On an individual live weight basis the species ranged in the following order: *E. minutus* and *E. macquariensis* (0.3 - 2.0 µg), *N. antarcticus* (0.2 - 8.5 µg), *Stereotydeus villosus* (Trouessart) (2.8 - 37.1 µg), *G. racovitzai* (4.4 - 115.5 µg).

Population respiration

Calculations of annual species population respiration have been made by a computer programme using data for monthly population density, life stage composition, live weight biomass, mean daily field temperatures and the relation of metabolic rate (weight specific oxygen uptake) to temperature for each species of arthropod on SIRS 1. Daily population respiration values were calculated and summed for annual estimates (Table 4). Differences in respiratory activity occur between species and years, the former governed principally by the metabolism - temperature curve and the latter by population density levels. Between year changes are exhibited by the total Acari data, the 1972 estimate being 1.7 times higher than the 1973 level. The total oxygen consumed by the Acari was almost all used by the Prostigmata. The Collembola (entirely *C. antarcticus*) contributed 80-84% of the total soil arthropod respiration for both years.

Life cycles and feeding

Information on life stage composition (Figure 4) has been obtained by Goddard (1979) and other workers for mites and by Tilbrook (1977) for springtails in the maritime Antarctic. In the Acari, several species have been observed to lay batches of eggs in spring and early summer, whilst others oviposit throughout the summer period. Larvae are abundant only in summer, whilst large numbers of nymphs of all stages are found at all seasons. The duration of the nymphal stages is variable, even within a species, which results in a mixed stage nymphal component of the population. From such a nymphal pool, varying numbers of individuals mature to adult influenced primarily by environmental conditions. Nymphs have been found to be more cold tolerant than adults in the oribatid *Alaskozetes antarcticus* (Michael) by Young & Block (in prep.), and so nymphal mortality may be low. In terms of time, 12 to 18 weeks from egg to adult have been observed for *Tydeus tilbrooki* (Strandtmann) at laboratory temperatures (Goddard, 1979). Under field conditions it may take at least one year for *A. antarcticus* to reach sexual maturity with a further 9 to 12 months of adult life. Life cycles are therefore variable in duration dependent upon site and microclimate.

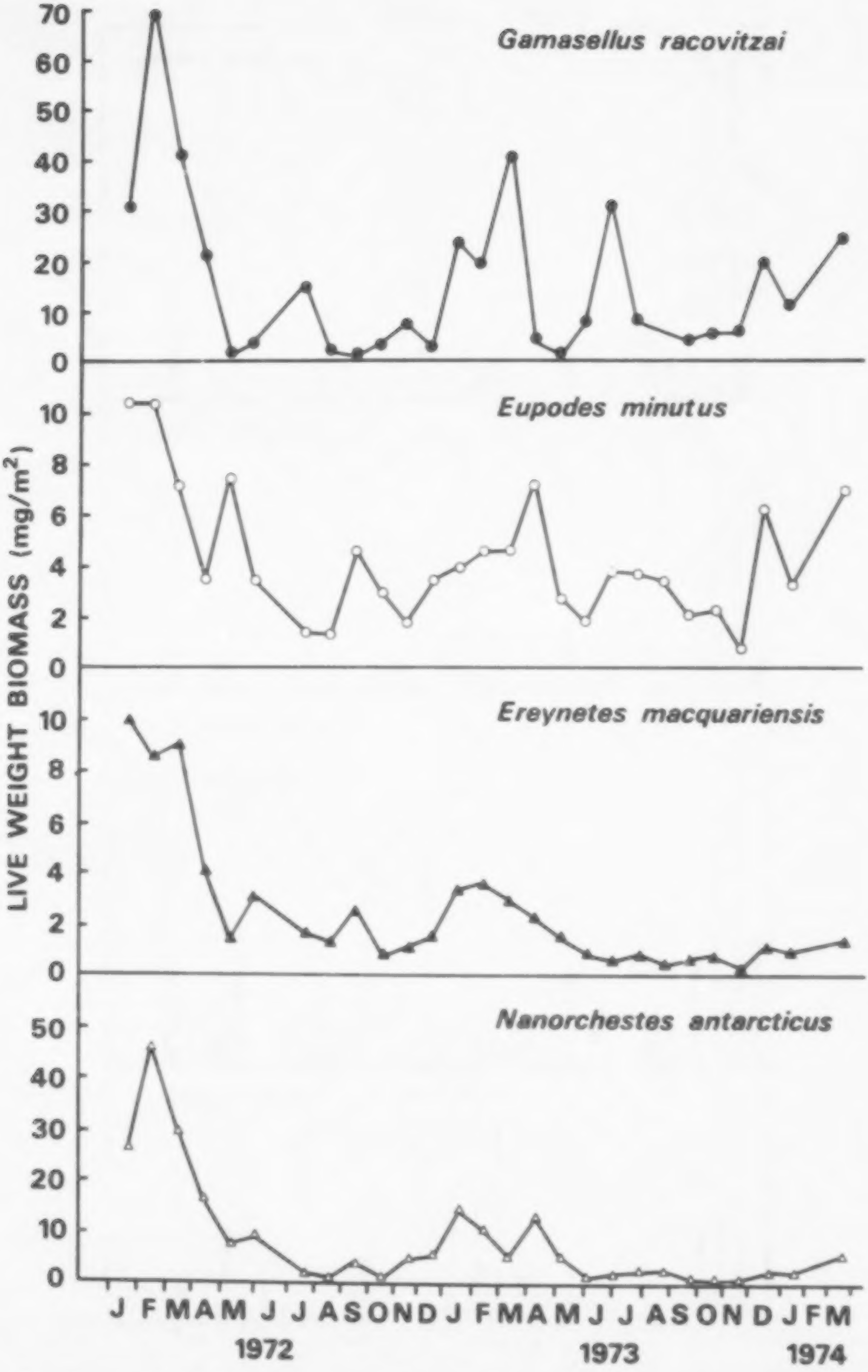

FIGURE 3. Live weight biomass changes in populations of four mite species on SIRS 1 during 1972-74.

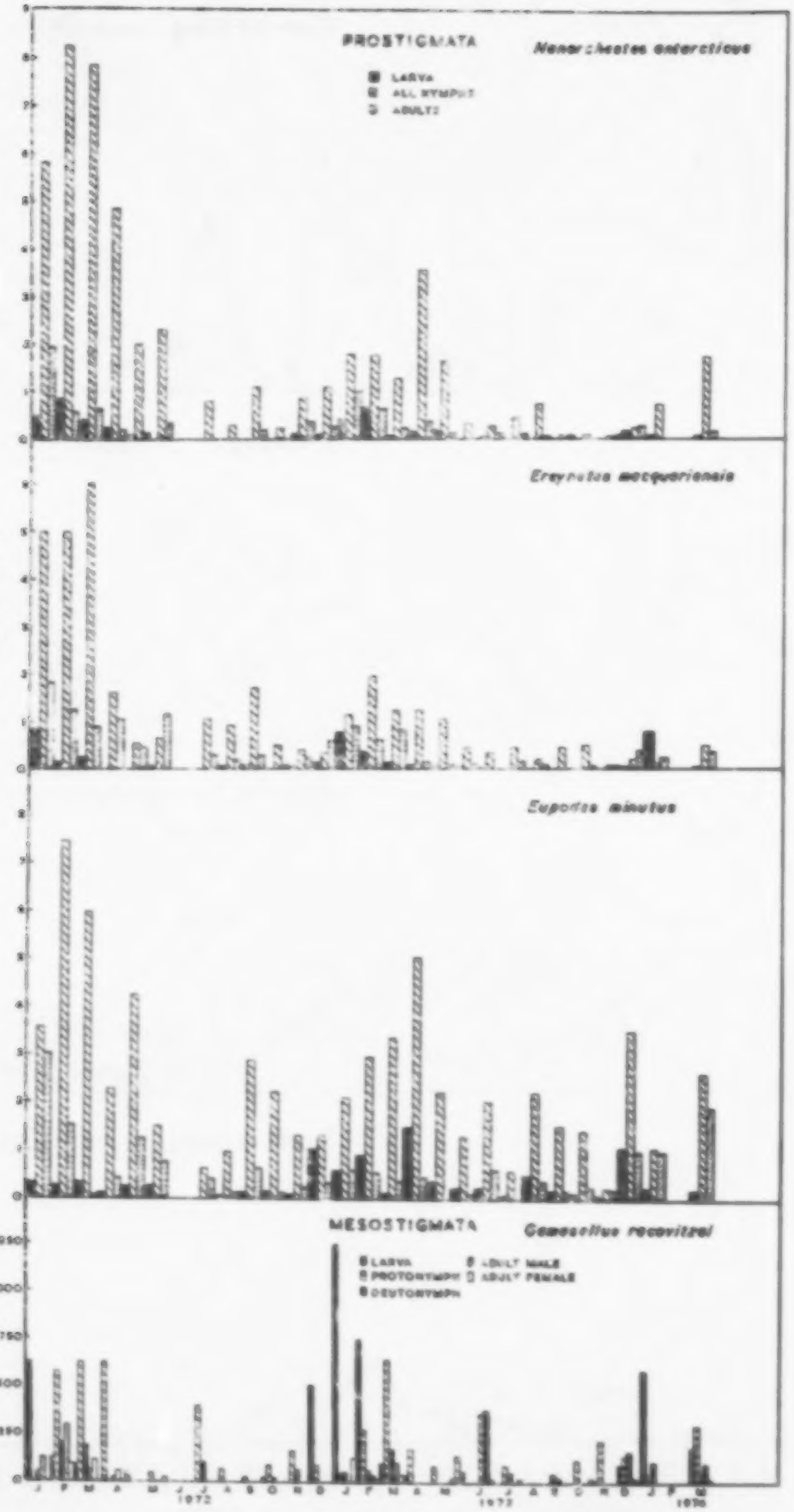

FIGURE 4. Life stage composition of four species of Acari on SIRS 1 during 1972-74.

TABLE 4

POPULATION RESPIRATION OF SIRS 1 ACARI AND COLLEMBOLA (ml O_2 m^{-2} y^{-1})

	Year	
Species	1972	1973
Ereynetes macquariensis	82.17	24.00
Eupodes minutus	43.87	29.94
Nanorchestes antarcticus	81.40	70.72
Gamasellus racovitzai	12.49	4.52
Total Acari	219.93	129.18
Total Collembola		
Cryptopygus antarcticus	893.35	685.84

For C. antarcticus, Tilbrook (1977) recorded a stable size class structure for the Signy Island population with few seasonal changes.

Few details of the feeding ecology of Antarctic soil arthropods exist. Observations at Signy Island suggest that algae and fungi are favoured by the majority of the Acari especially the prostigmatids (Table 5). Current work on C. antarcticus is to determine qualitative food preferences and measure ingestion and assimilation rates at field temperatures, whilst that on the predator, G. racovitzai, is investigating its interaction with various prey organisms.

Microclimate

Seasonal fluxes in solar radiation, air temperature and soil temperature at five points in the vertical profile of the SIRS moss peat have been given by Walton (1977). Temperature is a major determinant of arthropod activity, which on Signy Island is limited to c. five months of the year (November to March). The microclimate of the surface layer of the sites is characterized by short periods of high insolation with temperatures of up to +25° C being recorded in some situations, which are often associated with rapid temperature changes (1° C min^{-1} is common). Much longer periods of fairly constant low temperatures occur especially after a snow cover has been established (Figure 5). Snow depths vary between sites and between years, and up to 1 m may occur on bryophyte communities in the maritime Antarctic. At melt, greenhouse conditions may prevail locally, which encourage plant growth and invertebrate activity under the ice layer.

Of major importance for such communities are the frequent freeze-thaw cycles, which are a feature of both spring and autumn conditions. Substrate water content changes markedly with season particularly in peat sites. Annual water contents in respect of core dry weight were 609-666% (SIRS 1), and 1480-1842% (SIRS 2) for 1972 and 1973 respectively.

PHYSIOLOGY

The maritime Antarctic environment presents certain physiological problems to poikilotherms inhabiting it. Low temperatures may depress respiration rates, activity, feeding and growth, whilst wide thermal fluctuations may result in large variations in metabolic rates. Extreme winter temperatures may cause tissue freezing.

Respiratory metabolism

A considerable body of data now exists on the respiratory levels of many Antarctic arthropods. For Collembola, Block & Tilbrook (1975) and Block (1979) detail results for C. antarcticus and Parisotoma octooculata (Willem). In the Acari, Goddard (1977a, 1977b) gave information on G. racovitzai and the Prostigmata respectively, whilst Block (1977) and Young (1979a, 1979b) reported on the respiratory metabolism of the oribatid A. antarcticus in

TABLE 5

FOOD MATERIAL UTILIZED BY SPECIES OF ACARI AND COLLEMBOLA
IN THE FIELD AND IN LABORATORY CULTURES AT SIGNY ISLAND

Species	Type of food material					
	Collembola	Acari	Algae	Fungal hyphae	Lichens	Organic debris
MESOSTIGMATA						
Gamasellus racovitzai	+	+				
CRYPTOSTIGMATA						
Alaskozetes antarcticus			+	+	+	+
Halozetes belgicae			+	+	+	+
ASTIGMATA						
Neohyadesia signyi			+			
PROSTIGMATA						
Eupodes minutus			+	+		
Ereynetes macquariensis			+	+		
Stereotydeus villosus			+			
Nanorchestes antarcticus			+			
Tydeus tilbrooki			+	+	+	
ISOTOMIDAE						
Cryptopygus antarcticus			+	+	+	+

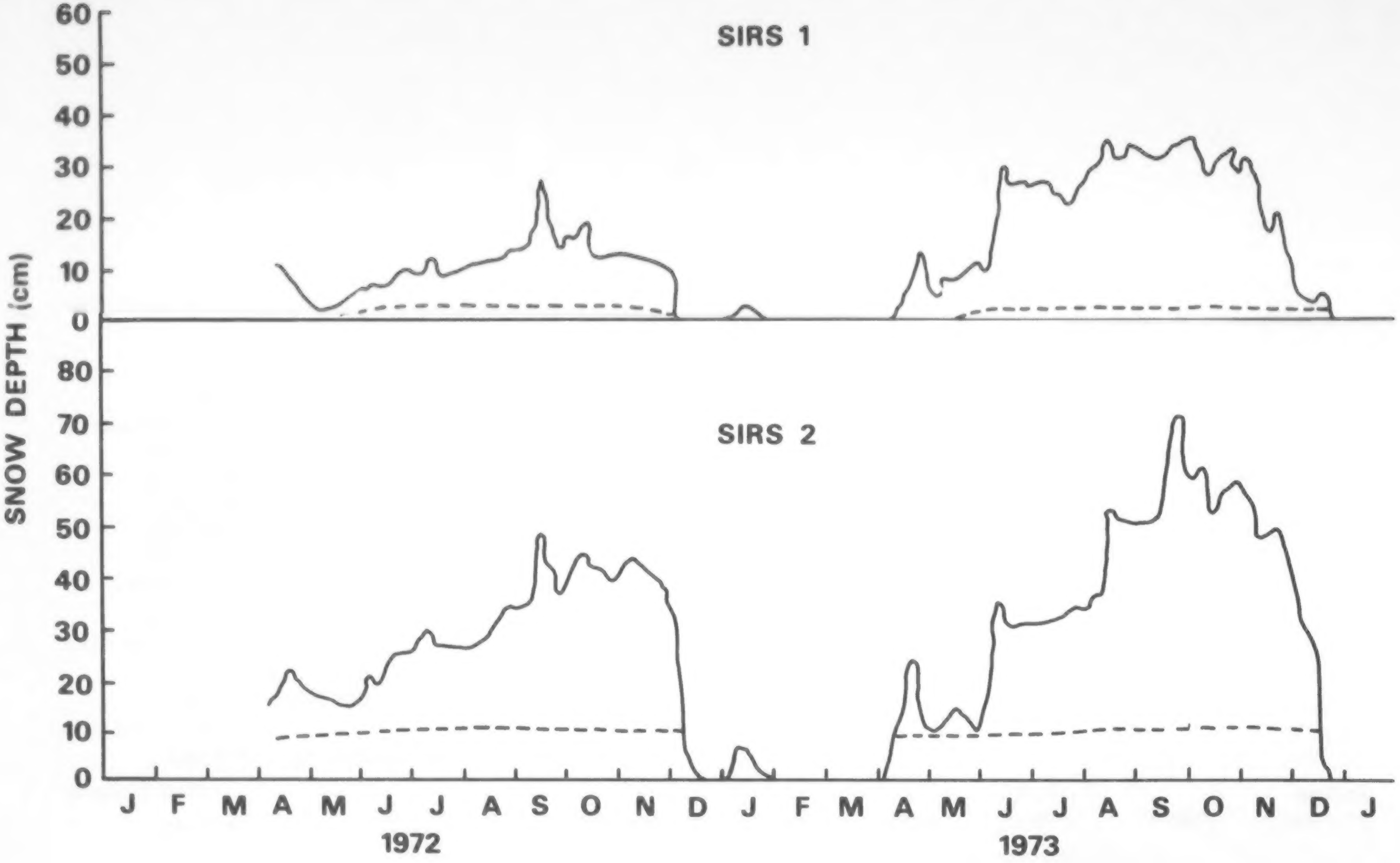

FIGURE 5. Mean snow depth of SIRS 1 & 2 during 1972-74. Dotted line represents approximate ice thickness.

field and culture. Data for this species supports the hypothesis of cold adaptation by metabolic rate elevation (Block & Young, 1978), in that its metabolic rate is higher than that of comparable temperate species measured at the same temperature. This enables the Antarctic mite to remain active at environmental temperatures that would immobilize those temperate forms. Such an adaptation is clearly of paramount use for this species, and similar metabolic phenomena may exist in other Antarctic species.

Overwintering survival

The limits of cold tolerance of several Antarctic mites have been examined (Block et al., 1978; Sømme, 1978), but a detailed investigation of the physiological and biochemical mechanisms involved has only been undertaken on a single species, *A. antarcticus* from Signy Island. Freezing is fatal in both juvenile and adult stages, and survival in the field takes place by means of the avoidance of freezing by supercooling (the maintainance of their body fluids as liquids below their freezing point). Food materials in the guts of individual mites has been shown to contain efficient ice nucleators and detract from supercooling ability (Young & Block, in prep.). Therefore animals with empty guts survive better under freezing field conditions. Glycerol aids supercooling in adult *A. antarcticus*, and this is supplemented by other polyhydric alcohols and sugars in the juveniles. Cold tolerance, as measured by glycerol concentrations and supercooling points, was increased to -30° C by exposure to low temperatures (0° to -10° C), and low relative humidity (40 to 60%), both of which can be related to its field habitat.

In Antarctic springtails, which are also freezing susceptible, similar limits of cold tolerance have been found (Block, et al., 1978), but sugars rather than glycerol appear to be the main factor for improving their supercooling ability.

CONCLUSIONS

The species considered in this short review are seen to be well adapted to their harsh maritime Antarctic environment, both in terms of their biology, ecology and certain of their physiological characteristics. The study of such Antarctic invertebrates is concerned essentially with the problems of adaptation, and the several facets of the adaptational strategy which are adopted by both the individual and the population. Much of what is known about the ecology of such forms suggest that they are ultimately controlled by environmental influences rather than interspecific competition. Until more information is available on the details of species biology, especially their trophic relationships, it is both difficult and dangerous to go further.

However, the physiological adaptations prompt various questions such as are these mechanisms novel and evolved in response to the polar environment, or are they merely extensions of pre-existing ones? Future work should be comparative, not only within the Antarctic Region, but also with similar forms from along climatic gradients such as cool temperate - sub-Antarctic - maritime Antarctic - Antarctic continental fringe. Such studies would indicate the ways in which polar soil faunas have developed and colonized habitats, and suggest the possible dispersal mechanisms employed by soil invertebrates.

ACKNOWLEDGEMENTS

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QUESTIONS and COMMENTS

K. RICHTER: Why do mites freeze more readily with a full gut content?

In extended constantly cool but not freezing weather the low gut content animal is favored. Can these animals survive with this limited food supply? If so, how? Wouldn't they have to extensively feed to build up reserves prior to brumation to survive the cold period?

W. BLOCK: Gut contents contain ice nucleation agents, especially small particles, and water which promote freezing of individual mites in the supercooled state.

No, the low gut content animal is only favoured during subzero temperatures. The Antarctic species studied to date are able to overwinter without much food being ingested, but reserves are probably built up during summer to allow this to occur. We have some current research on this topic in the British Antarctic Survey.

M. HASSALL: With respect to those species which showed clear differences in population density between the two years studied could you please tell us what is the average life span of these species and could you speculate on the reasons for the observed differences in density?

Do the species with glycerol in the body fluids show seasonal differences in glycerol content? If so, do you know which stimuli trigger off the physiological response of glycerol production?

W. BLOCK: We have no information on the life span of these species. The between year differences (mainly a reduction in the second year) could have been due to a high winter mortality. Subsequent sampling suggests that the decline observed was not permanent.

We have some preliminary data which show seasonal fluctuations in glycerol levels in the mite *Alaskozetes anarcticus*. Low temperature, lowered RH levels both stimulate glycerol production in this species.

L. BENNETT: Is the cold adaptation of Anarctic mites aided by the sugar trehalose?

W. BLOCK: Trehalose has been found in both Collembola and mites from the Antarctic, but there is no quantitative information available. In general, juveniles of the cryptostigmatid mite *Alaskozetes antarcticus* appear to employ sugars as well as a variety of polyhydric alcohols in their cold tolerance physiology, whereas the adults rely almost entirely on glycerol.

DESERT SOIL MICROARTHROPODS AN 'r'-SELECTED SYSTEM

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INTRODUCTION

Hot desert soils and their inhabitants represent relatively simple ecological systems. Microarthropods feature prominently in such systems, and they have been the subject of increasing attention by biologists during the last decade or so (Wood, 1971; Wallwork, 1972a, 1972b; Edney, Franco and McBrayer, 1976; Johnson and Whitford, 1975; Schumacher and Whitford, 1976; Whitford, 1976). As a result of these studies, much information is accumulating on the species composition, population densities, spatial distribution, and the role of soil animals in decomposition in hot deserts. With this information comes an increasing awareness of the strategies which permit microarthropods to survive in the inhospitable environment of the hot desert soil. This paper presents a preliminary analysis of data from one desert site, and a synthesis which suggests that a strategy for survival does exist, which conforms to that elucidated in current ecological theory.

ECOLOGICAL STRATEGIES

Two basic, and contrasting, life styles are recognised: 'r' and 'K' strategies (Pianka, 1970). These two categories are not absolute in that a particular species population may not fit neatly into one or other of the two; it may display attributes of both. Again, a particular taxonomic group, such as oribatid mites or Collembola, may exhibit 'r' selection under one set of environmental conditions and 'K' selection under a different set. Again, generalisations about an ecological system must be made with caution since it is conceivable, for example, that a predator may be an 'r' strategist while its prey may be 'K' strategists.

Despite these reservations, the broad concept of 'r' and 'K' life styles can be applied in the present analysis and before developing this further, it is pertinent to recall the contrasting features of these two strategies.

'r' selected

1. Live in unstable/unpredictable environments.
2. Are early colonisers.
3. Are opportunists living in non-competitive situations.
4. Are short-lived; have high reproductive rates and short development times.

5. Usually occur in low densities which change erratically.
6. Equitability, or 'evenness' component of species diversity is low.

'K' selected

1. Live in stable environments.
2. Are late colonisers.
3. Are specialists living in competitive situations.
4. Are long-lived; have low reproductive rates and long development times.
5. Have stable populations at or near carrying capacity.
6. Equitability component is high.

STUDY SITE

Sampling was conducted over a nine-month period in the Joshua Tree National Monument, Riverside County, California from October 1966 until June 1967, at a site where juniper bushes provided enough protection from wind and water to allow a permanent litter layer to develop. A detailed description of this site, together with ecological data on its soil microarthropod fauna have been published previously (Wallwork, 1972a) and need not be repeated here.

ANALYSIS AND ARGUMENT

What follows is a re-examination of the Joshua Tree data within the broader conceptual framework of survival strategies. This can be carried out by applying, in turn, each of the six criteria listed above.

Stability and predictability

It has been argued (see Noy-Meir, 1973) that the 'level-controlling-flows' paradigm, which adequately describes each compartment in a cool, moist temperate ecosystem model is less appropriate to hot deserts than the 'pulse and reserve' paradigm. Essentially, the difference between these two modules is that the former describes continuous processes and variables, the latter discrete events.

According to the 'pulse and reserve' paradigm, an environmental variable triggers off a pulse of biological activity, of growth and reproduction. Much of the production occurring during this time is lost due to mortality, but some is channelled into a reserve - seeds in the case of plants, eggs or aestivating stages in the case of animals. This reserve is, essentially, a no-growth compartment from which the next pulse of activity originates.

The driving environmental variable in hot deserts is rainfall, and pulses of biological activity are closely linked to rainfall events. Figure 1 clearly indicates that this is true for the microarthropods in the Joshua Tree site. Here, there is an immediate biological response to a December rainfall manifested by a virtual doubling of population sizes. This moisture input will have its most obvious effect on the environment of the soil surface, in this case the litter layer. Figure 2 shows that densities of microarthropods

FIGURE 1. Monthly variation in microarthropod numbers in a juniper soil: litter and mineral soil counts combined (each value is a mean of 8 ccres).

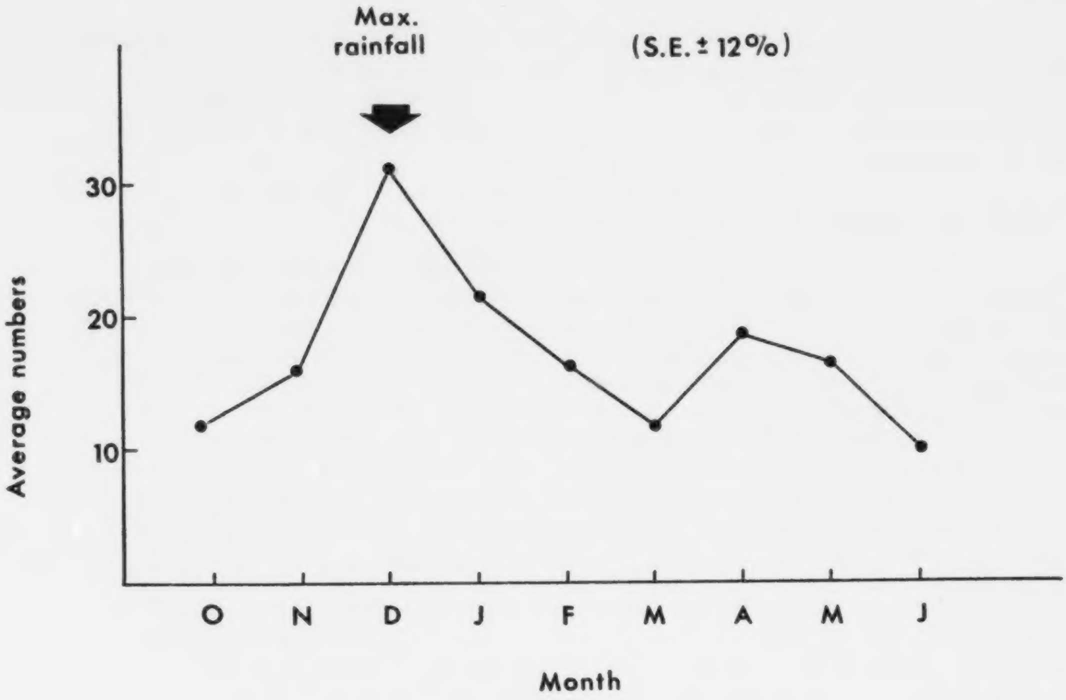
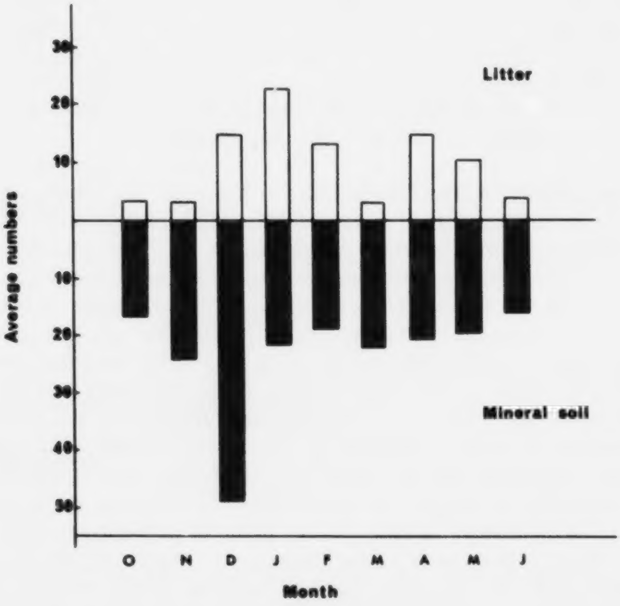


FIGURE 2. Monthly variation in microarthropod numbers in juniper litter and mineral soil.



increase in the litter in the December to February period and, after a decline in March, produce a second peak in April and May. These population peaks coincide with periods of recruitment, as will become apparent shortly.

Rainfall events are discontinuous and stochastic in hot deserts; their timing and magnitude have a large random component. Hence, desert soil microarthropods can be said to live in, and respond to, an unpredictable environment, thus satisfying the first criterion for an 'r' selected system.

Faunal succession

A total of 33 microarthropod species was recorded from the Joshua Tree site, mainly oribatid and prostigmatid mites and Collembola. In the context of 'r' and 'K' strategies, it is necessary to establish whether or not this constitutes a 'pioneer' fauna. This requires a knowledge of faunal succession which cannot be obtained from a nine month sampling program and, in the absence of empirical data, it is necessary to seek theoretical explanations. Two categories of evidence are relevant here. Firstly, the soil at the Joshua Tree site consists of a surface layer of juniper needles lying directly on a quartzitic mineral layer - with no intervening humus or fermentation layers. This is, essentially, an embryonic stage in soil formation and, intuitively, it could be expected that its fauna would be a pioneer one. Secondly, oribatid and prostigmatid mites and Collembola are often early colonisers of developing soils, particularly those of a mineral character, in many parts of the world, and it is perhaps no surprise that, collectively, these groups contribute nearly two-thirds of the microarthropod species recorded from the site.

Opportunism

It has been shown (Wallwork, 1972*a*) that the December peak in the population curve depicted in Figure 1 is largely caused by the influx of an astigmatid mite, *Glycyphagus* sp., into the mineral soil (see also Figure 2). This mite is phoretic as a hypopus on insects, and this mode of life is, essentially, an opportunistic one. Its ability to flourish in an environment which places a premium on opportunism indicates that it is an 'r' strategist.

The most abundant oribatid mite on this site, *Joshuella striata* Wallw., is also an opportunist. Its life cycle is geared to the December rainfall, such that a new generation of individuals appears at this time and in the following months of January and February (Wallwork, 1972*a*). Opportunistically, *J. striata* takes advantage of the wettest months of the year to produce juvenile stages which will be exposed to the least environmental stress. The second most abundant oribatid at this site, *Haplochthonius variabilis* Wallw., does not respond with such immediacy to December moisture; it recruits mainly in the months of April and May. In this sense, *H. variabilis* appears to be less opportunistic than *J. striata*, but it must be pointed out that there is still an appreciable amount of moisture present in the litter (where these juveniles are exclusively found) during April and May. Moreover, the temporal separation of recruitment periods for *J. striata* and *H. variabilis* may be interpreted as a device to eliminate competition between these two saprovore species. This, again, is a characteristic of an 'r' strategy.

The main microarthropod predator in this system appears to be the prostigmatid mite Spinibdella cronini (Baker and Balcock) and it has been shown to prey on juveniles of both of the oribatids mentioned above. Here, it displays real opportunism, as the curves in Figure 3 illustrate. The prey curve, in this Figure, is a composite derived by pooling the monthly population estimates of J. striata and H. variabilis, and its bimodality reflects the different contributions made by these two species to total microarthropod numbers at different times of the year. The lower curve in the Figure shows monthly variations in the numbers of S. cronini and, again, this curve is bimodal. The two peaks coincide with two periods of recruitment (Wallwork, 1972a), and it is obvious that one of these corresponds to that of one of the prey species (the January peak for J. striata), and the other, and larger, peak to the April/May recruitment of H. variabilis. This is no classical predator/prey curve for there is no lag phase in the build-up and decline of populations of prey and predator. The predator has been able to gear its life cycle to correspond exactly with the prey cycles. This implies that the predator population is not food-limited and, hence, will not be competing with any other predators on the site for food. It can be concluded that S. cronini is an opportunist living in a non-competitive situation - as befits an 'r' strategist.

Reproductive strategies

It will be clear, from what has been said above, that the three species of mite which constitute an important numerical part of the microarthropod fauna in Joshua Tree have periods of recruitment which are largely restricted to one or two months of the year. At other times of the year, the populations are composed almost entirely of the adult stage. This immediately suggests that post-embryonic development to adulthood is rapid. It was previously noted (Wallwork, 1972a) that, in contrast to the adults which were recovered mainly from the mineral soil at depths of 8-14 cm, juveniles of all three of these mite species occurred mainly in the surface litter layer. Juveniles apparently migrated upwards from the mineral soil into the litter after hatching, and this dispersal activity would bring these immatures into regions of higher temperatures which would accelerate post-embryonic development. Rapid development times are characteristic of 'r' strategists, and another of the criteria set out at the beginning of this paper is partly satisfied. To satisfy this criterion completely, data are required on reproductive rates and longevity. These are not available, but in the case of longevity, an inference can be made. As noted above, for most of the year populations of J. striata, H. variabilis and S. cronini consist virtually of adults. There is not the mixture of age classes in the populations which would characterise species with overlapping generations. It may be concluded, then, that generations do not overlap and are, therefore, short-lived - another 'r' strategem. Indeed, in the case of Haplochthonius variabilis, the available data suggest a complete separation of generations since, after a peak in adult numbers in November, the species is hardly encountered again in samples until the start of its recruitment period in the following April.

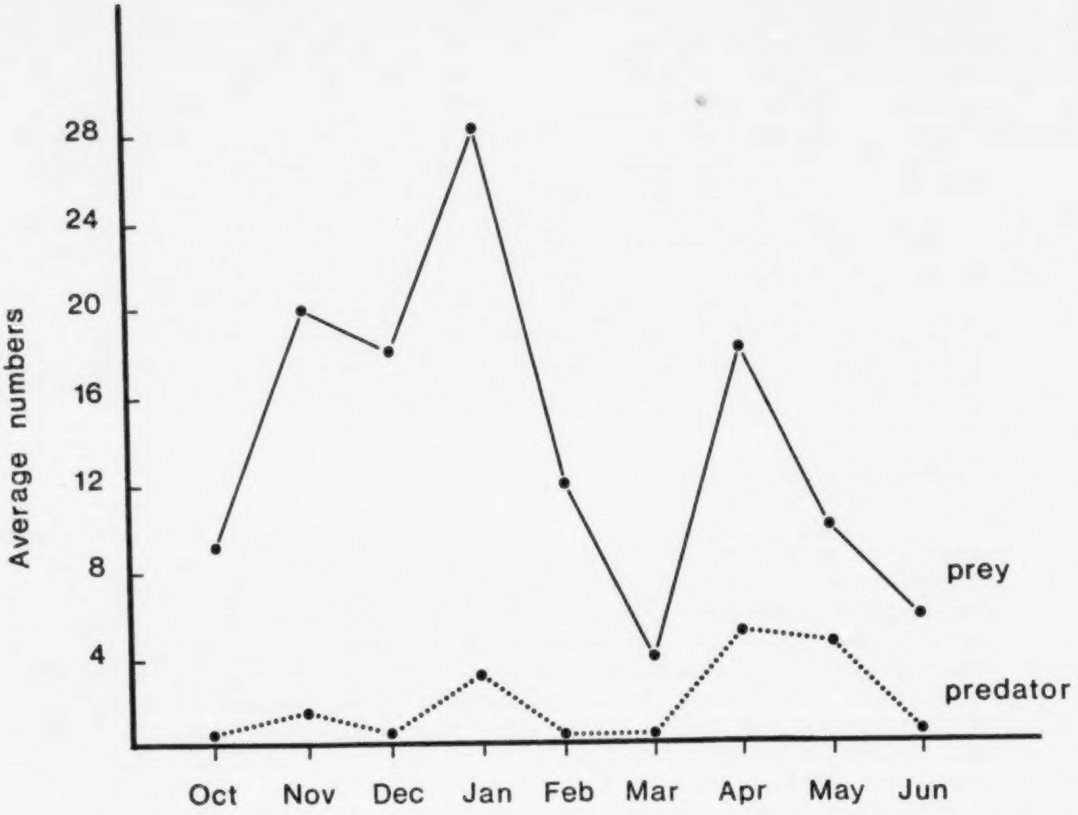


FIGURE 3. Population curves for a predator/prey system in juniper soil. Upper curve is obtained by pooling counts for *Joshuella striata* and *Haplochthonius variabilis*; lower curve is for *Spinibdella cronini*.

Population densities

Low densities for microarthropods in desert soils were first reported by Wood (1971) (Australia) and Wallwork (1972a) (North America). More recent studies in North American deserts are very much of the same order of magnitude as these earlier estimates, as shown in Table 1. For purposes of comparison, Table 1 also includes a range of microarthropod densities reported by various workers from a variety of cool, moist temperate, lowland grasslands. Clearly densities of desert microarthropods are lower, in general, by a factor of ten, than their counterparts in other parts of the temperate region.

TABLE 1. Densities of microarthropods in different desert soils compared with cool moist temperate grasslands.

Locality	Avr. nos. $(\times 10^3, m^{-2})$	Authority
Desert grassland, Australia	2 - 3	Wood (1971)
Juniper soil, Mojave	1.6	Wallwork (1972a)
Mojave litter, various	1 - 13	Edney, Franco and McBrayer (1976)
Chihuahuan litter, various	0.146 - 3.1	Santos, DePree and Whitford (1978)
Cool temperate grasslands	32 - 298	Wallwork (1970)

These low population densities in deserts are another indication of an 'r' selected system. Not enough data are available to determine whether or not populations within a particular site show erratic density changes; a long-term sampling program is required for this purpose. However, Santos et al. (1978) have shown that there is a high correlation between microarthropod densities and the amount of surface litter present. The distribution of surface litter in the Chihuahuan sites studied by these workers is very much influenced by surface run-off of water during heavy rains. Hence, it could be argued that microarthropod densities may be influenced, perhaps indirectly, by physical factors which are stochastic in character. If densities respond in a similar stochastic manner, it could be expected that changes will be unpredictable in their timing and magnitude. The hypothesis that microarthropods respond to physical parameters in the desert environment receives some support from a consideration of equitability ratios.

Equitability

The concept of 'equitability' (Lloyd and Ghelardi, 1964) relates the way in which the total number of individuals are distributed among the total number of species present on a site. The observed distribution of individuals among species is compared with the 'broken stick' model of MacArthur (1957) which apportions individuals among species about as equitably as is possible in nature. The extent to which an observed distribution departs from MacArthur's model will be measured by the extent to which the equitability ratio falls below unity. According to Lloyd and Ghelardi (1964), equitability is sensitive to the stability of physical conditions, and 'r' selected systems have relatively low equitability ratios.

Estimates of the various parameters required for the calculation of equitability in the Joshua Tree site are presented in Table 2. These estimates are based on data from 20 species of mites and Collembola and, thus, are directly comparable with estimates provided by Lloyd and Ghelardi (1964) for soil microarthropods in a temperate beech forest.

TABLE 2. A comparison of diversity parameters from temperate forest and hot desert (Mojave).

	Temperate forest	Hot desert
s	44	20
H_{max}	5.46	4.32
H	4.16	2.66
s'	26	9
e	0.59	0.45

where:

s = the observed number of species

H_{max} = the maximum diversity obtainable if all species were equally abundant

H = the observed species diversity (Shannon-Wiener)

s' = the theoretical number of equally abundant species which would be required to give the observed species diversity.

e = the measure of equitability; the ratio s'/s

It is evident that equitability is lower in the hot desert Mojave site than in the temperate beech forest. In other words there is an appreciable departure from the MacArthur model.

CONCLUDING REMARKS

All of the evidence presented in this paper strongly suggests that the soil microarthropods of a juniper site in the Mojave desert exhibit characteristics of an 'r' selected system. The ecological significance of distinguishing between 'r' and 'K' selected systems is that, in the former, emphasis is placed on productivity, whereas efficiency is the hallmark of the latter. 'r' selected systems have a high rate of turn-over of biological materials and, looked at in terms of the decomposition process occurring in the soil, this means a high rate of nutrient release and a rapid depletion of these nutrients through leaching. This is reflected in the low organic content of hot desert soils and may explain why, in the profile under juniper at the Joshua Tree site, discrete fermentation and humus layers are absent.

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QUESTIONS and COMMENTS

P. LAVELLE: I have studied earthworm communities along a decreasing rainfall gradient in West Africa. I find that the most humid ecosystems have communities composed of r and K species. Then, when rainfall decreases K species disappear. Do you think desert ecosystems could be considered as systems reducted to r components?

J.A. WALLWORK: As far as our present knowledge is concerned, I do indeed believe that this is the case in hot deserts. However, I am not sure that this applies equally to cold deserts; more data must be obtained from these before any firm conclusions can be drawn.

M.S. GHILAROV: What was the maximum depth of soil layer you have examined? In the desert microarthropods can exist at significant depths where conditions are rather stable and selection is of K-type (Examples of larger forms are Hemolepistus woodlice).

J.A. WALLWORK: I sampled to a depth of 14 cm, and I agree that this procedure may have neglected deep-dwelling species which, indeed, may be K-selected. However, my primary interest was with that part of the soil ecosystem associated with the surface litter and the mineral soil immediately beneath this litter, for it is here that the major part of organic decomposition is occurring.

M. HASSALL: With respect to your suggestion that the predatory species you described are not food limited, may there be a parallel here with the herbivore systems in African grasslands, described by Sinclair (1975) who found that although primary production of food species was well in excess of the amount consumed by herbivores, the herbivores were still food limited because of seasonal discontinuities of food supply. Is there a possibility that food could similarly be limiting the predatory species in the desert where prey species are at a minimum e.g. during March?

J.A. WALLWORK: This is possible, but I don't think it is probable. In fact, there is no short answer to this question. In a global sense, I do believe that herbivores are predator-limited, rather than food-limited. Again, by the same token. predators are limited by their food supply in a global sense. But the desert system that I have been studying, the absence of a lag phase in prey and predator population increases does not suggest a negative feedback at the times of population recruitment. As M. Hassall rightly points out, however, there may be periods of the year when predators could experience food shortage, and limiting effects could then come into the picture. I would suggest that the predatory species Spinibdella cronini responds to this situation in one (or both) of two ways. Firstly it does not recruit during periods of food shortage. Secondly, it avoids such periods of food stress by mobilizing food reserves laid down during times of plenty. While I have not been able to demonstrate that S. cronini does in fact do this, I have established elsewhere that predatory mites can make this provision. If S. cronini follows this pattern, it need not experience periods of food stress, and its subsequent fecundity would not be impaired.

B. STEVENSON: Do seasonal "pulses" in annual desert climate produce changes in carrying capacity (e.g. does rainfall increase K for microarthropods)? Is it possible for arthropods to track (with changes in population density) changes in K?

J.A. WALLWORK: My observations in the Mojave cannot provide an answer to this question, for I was not able to establish what was the carrying capacity of the system. I am able to say that population densities of microarthropods are lower than in cool, moist, temperate ecosystems but the important part to establish, which I did not, was whether these densities were low in relation to the carrying capacity; this determines the type of strategy employed, and if my case rested on this criterion alone, it would be hardly defensible. However, it does not, and in the event, work in progress has shown that microarthropod densities will increase in artificially watered plots, and in sites immediately subjected to rainfall. So, the answer to both your questions is an affirmative: yes, environmental pulses produce changes in carrying capacity, and yes, microarthropods can track these changes. This is an opportunistic strategy.

M.J. MITCHELL: Do you have any information on whether specific population "r" or "K" characteristics, such as fecundity or rate of increase have been selected for in the arthropod populations?

J.A. WALLWORK: No, the scope of my investigation did not allow for estimates of fecundity or rates of increase in populations.

ARTHROPODS AND DETRITUS DECOMPOSITION IN DESERT ECOSYSTEMS

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INTRODUCTION

The mountain and basin topography of the desert areas of North America has a profound effect on the distribution and redistribution of dead plant material (litter). Topography has an effect on density and species composition of vegetation especially along water courses and redistribution of litter by sheet flow of water and by wind. Litter accumulates under shrubs and along edges of water courses and is buried in depressions or where snags, rocks or obstructions create wind and water eddy currents. Santos, DePree and Whitford (1978) have shown that the density and diversity of the soil microarthropod community varies directly with the amount of organic matter present, hence, are directly related to topography.

Studies of the soil fauna of the worlds' deserts are limited (Wallwork, 1970, 1972; Wood, 1971; Freckman, Mankau, and Ferris, 1975) and there have been no quantitative studies of the role of soil fauna in decomposition and nutrient release from plant litter. In 1977 we initiated a series of studies to examine the roles of various taxa of desert soil fauna in decomposition and in mineral release processes. In this paper we review selected portions of these studies in order to illustrate the relationships of termites, microarthropods, nematodes and soil microflora in litter decomposition in North American desert ecosystems.

STUDY SITES

Most studies were conducted on the New Mexico State University Experimental Ranch 40 km NE of Las Cruces, NM. The study site is an alluvial pediplain (bajada) of Mt. Summerford drained by a large dry wash (arroyo) and dissected by numerous smaller arroyos which empty into the main drainage channel. The large arroyo drains into a dry lake at the base of the watershed. The alluvial fan has a vegetative cover of approximately 27% of which creosotebush, Larrea tridentata, accounts for 89%. The subdominant shrubs are mesquite, Prosopis glandulosa, 1.05% cover; tarbush, Flourensia cernua, 1.00% cover and snakeweed, Gutierrezia spp., 0.65% cover are located at the edges of the arroyos. Summer air temperature maxima vary between -5°C and 10°C. Mean summer (May-September) soil temperatures at 10 cm vary between 25°C and 37°C in the summer months. The 100 year average annual rainfall

± one standard deviation is 211 ± 77 mm (Houghton, 1972) with most of that rainfall occurring in July-September from convectional storms.

Four additional sites were used to compare microarthropods and bacteriophagic nematodes in North American hot deserts. The Sonoran desert site is a sloping alluvial pediplain of the Sierra Estella Mts. 32 km west of Casa Grande, Arizona. The bajada is dissected by several small arroyos. The vegetative cover was visually estimated at 20% with a mixture of creosotebush, *Larrea tridentata*; palo verde, *Cercidium microphyllum*; sagauro cactus, *Cereus giganteus*; and ironwood, *Olneya tesota*. Summer temperature maxima regularly reach 40°C. Average annual rainfall is about 206 mm with both winter and summer precipitation.

The Coloradan desert site is 3 km east of Glamis, California on a gravel-rock pavement with a sparse (less than 5%) cover of cresotebush, ironwood and *Encelia farinosa*. Here the summer temperature maxima regularly exceed 40°C and average rainfall is 68 mm with most of that falling between December and March.

The Mojave desert site is 30 km ESE of Boulder City, Nevada on a gently sloping bajada dissected by numerous small arroyos. Vegetative cover is around 20% most of which is creosotebush with *Yucca schottii* as subdominant. Summer temperature maxima range between 38°C to 40°C; the average annual precipitation is 131 mm primarily in the winter months.

METHODS

All of the decomposition studies reported herein utilized fiberglass mesh bags initially containing 30 gms of litter for surface bags and 20 or 30 gms for buried bags. Arthropods were excluded from litter bags by treating the litter with the insecticide chlordane (TM). The litter was either mixed litter (termite studies) containing about 60% creosotebush (*Larrea tridentata*) and pieces of grass and forbs or just creosotebush litter which consisted of freshly picked, air dried leaves and small twigs. Bags were placed on the surface under the canopy of creosotebushes or buried 15 cm below the soil surface under creosotebush canopies.

Microarthropods were extracted in modified Tullgren funnels into water and counted within 24 hours after extraction was completed (usually 72 hours). Nematodes were extracted from the litter by a combination of the Cobb sieving method and the Oostenbrink cotton-wool filter (Nichols, 1975).

Organic matter loss was determined by ashing oven dried contents in a muffle furnace and correcting for mean initial organic content of the sample and organic content of the soil in the area where bags were placed. Bacterial numbers were estimated by direct counts of cells of homogenates of plant material stained with Acridine orange and counted with a UV microscope.

RESULTS

In mixed litter during the period of peak surface foraging by the subterranean termites, Gnathamitermes tubiformans, surface bags in which termites foraged as evidenced by galleries below the bags and carton in the bags, lost 57.4 ± 7.7% of the initial weight, while bags in which termites were excluded lost 32.3 ± 4.6% of the initial weight. This experiment was conducted from mid-August through October.

Litter bags buried from the end of July through October lost 42 ± 10% of the original organic matter. The microarthropod community in surface bags during that period was more diverse but the taxa in buried bags occurred in significantly greater densities (Table 1). Mixed litter buried for 90 days had a fauna dominated by tydeid and pyemotid mites and Psocoptera. There were no clearly dominant microarthropods in surface litter (Table 1). However, most of the surface litter mites were predatory Prostigmata.

TABLE 1. Comparison of microarthropod communities in 30 gms of mixed creosotebush litter in buried and surface bags July-October. Numbers are mean numbers ± standard deviation per bag. Buried N = 10, Surface N = 8.

TAXA	BURIED	SURFACE
Cryptostigmata		
Oribatid		3.8 ± 0.4
Prostigmata		
Tetranychidae		1.3 ± 0.8
Tydeidae	200 ± 35	3.5 ± 3.0
Pyemotidae	499 ± 65	
Tarsonemidae	9 ± 7.6	5.3 ± 2.2
Nanorchestidae		7.8 ± 0.8
Bdellidae		4.3 ± 1.2
Smaridiidae		1.1 ± 0.7
Cunaxidae		0.8 ± 0.5
Mesostigmata		
Rhodocaridae	9 ± 3.3	
Laelapidae	3.1 ± 1.4	
Psocoptera		
Liposcelidae	44.4 ± 5.3	3.1 ± 1.2
Trogiidae		7.4 ± 3.2
Collembola	8.5 ± 5.8	0.2 ± 0.2

In experiments in which we examined the effect of eliminating microarthropods on organic matter loss and other components of the litter decomposer community, we found that the initial mite colonizers were tydeid mites which entered the buried litter within 5 to 10 days after burial. After 10 days, insecticide treated bags had significantly higher populations of bacteriophagic nematodes, lower numbers of bacteria and significantly less organic matter loss (Table 2).

TABLE 2. The effect of eliminating Tydeidae mites from buried litter on other components of the litter system and on organic matter loss in 30 gms of creosotebush litter buried for 10 days.

	UNTREATED			Insecticide (chlordane) TREATED		
	$\bar{x}$	±	SD	$\bar{x}$	±	SD
Tydeidae (no./bag)	85	±	25		0	
Bacteriophagic Nematodes (no./bag)	109	±	52	600	±	225
Bacteria (no./gm litter)	3.3×10^6			2.0×10^6		
Organic matter loss	20.7	±	2.3%	5.6	±	2.5%

Except in the hottest and driest desert, the Coloradan, we found that eliminating the microarthropods resulted in a significant increase in free living nematodes (Table 3). Buried creosotebush litter in the Coloradan desert also had significantly lower microarthropod populations than in the other hot deserts. The faunas in buried litter in the Sonoran, Mojave and Coloradan deserts differed from the Chihuahuan by the absence of tarsonemids which were the most numerous mites in the material from the Las Cruces, NM area (Table 3). Also liposcelid psocopterans were absent in the two month buried bags from the Chihuahuan area and predominant in the buried bags from the other deserts (Table 3). However, liposcelid psocopterans were present in the Chihuahuan area in three month buried bags (unpublished data) and were always found associated with collembolans which were not present in the other deserts. Raphignathidae are the most common predators in the Sonoran, Mojave and Coloradan deserts (Table 3). There was a great diversity of predatory mites in the Chihuahuan desert. Raphignathids were part of the predatory complex in bags buried for 90 days in the Chihuahuan desert area (unpublished data). The taxon common to all of the deserts in the two month buried bags was the tydeid mites which are the first colonizer and apparent nematode predators.

TABLE 3. A comparison of free living nematodes and soil microarthropods extracted from buried 20 gm creosotebush litter in selected North American desert sites. Numbers reported are numbers per litter bag. Two litter bags from each site were extracted for nematodes and three extracted for mircoarthropods.

	Chihuahuan Las Cruces, NM	Sonoran Casa Grande, Arizona	Coloradan Glamis, California	Mojave Boulder City, Nevada
Nematodes (NT)	50- 161	394- 1050	416-3774	3600- 3878
Nematodes (IT)	1937-2155	6395-11164	968-1050	11800-12408
Tydeidae -	156 ± 36	17.3 ± 4.2	3.3 ± 1.52	8.25 ± 5.56
Tarsonemidae -	7345 ± 1681	—	—	—
Raphignathidae -	—	17 ± 5.5	1.3 ± .57	19.5 ± 13.4
Liposcelidae (Psocoptera) -	—	153 ± 87	12 ± 2.3	126 ± 75
Other predatory mites -	461 ± 167	—	—	—

Period March 14, 1979 to June 1979.

DISCUSSION

Johnson and Whitford (1975) estimated that on the Jornada subterranean termites consumed 5.6 x 10^6 cal·ha^{-1} and that total detrital input including cattle dung and rabbit feces was 10.3 x 10^6 cal·ha^{-1}. Their estimates were based on paper consumed from toilet paper roll baits. Fowler and Whitford (unpublished data) showed that termites did not utilize creosotebush leaf litter. Data reported here suggests that termites harvested the annual forb-parts and bits of grass from the mixed litter, leaving the creosotebush leaves to be broken down by the other desert litter feeders. *Gnathamitermes tubiformans* builds gallery tunnels into surface accumulations of litter and transports pieces of litter material to some unknown depth in the soil. In late summer and autumn when relative humidity varies between 50% and saturation, *G. tubiformans* builds galleries around standing dead vegetation which is completely harvested. However, since annual forb production is only around 4 kg·ha^{-1} depending on rainfall (Whitford, 1973), organisms that process the leaves of creosotebush must be more important to the nutrient cycling economy of this system than the subterranean termites. Data on forage selection of *G. tubiformans* suggests that the consumption rates estimated from bait rolls overestimate consumption of natural plant materials. However, these must be considered tentative conclusions and must await additional data on the role of termites on decomposition processes.

Although there was a higher diversity of microarthropods in surface litter bags than in buried bags in late summer, microarthropods are completely absent from surface litter during some parts of the year. It is possible that there is a diel migration of microarthropods from the soil into surface litter and back into the soil depending upon the moisture and thermal gradients between soil and litter. The predominance of predatory mites in surface litter suggests that there may be significant populations of nematodes in surface litter but this remains to be documented. The predominance of tydeid, tarsonemid and pyemotid mites in buried litter and the higher population numbers probably result from the more constant and favorable temperature and moisture conditions of buried litter in comparison to surface litter.

We have both indirect and direct evidence that tydeid mites prey on nematodes. In the mite exclusion experiments, bacteriophagic nematode numbers were 6X greater in the insecticide treated bags when tydeid mites were excluded. We have observed tydeid mites feeding on nematodes in laboratory culture. We suggest that these mites affect organic matter breakdown by preying on bacteriophagic nematodes which reduce the primary decomposers: the bacteria.

The reciprocal relationship between mites and nematodes is common to the wetter North American deserts but appears to break down in the driest deserts. At the time of this writing climatological data for the Arizona and Nevada reporting stations was available only through March 1979 (National Oceanic and Atmospheric Administration Climatological Data, National Climatic Center, Ashville, NC). The March data show Casa Grande, Arizona receiving 30.2 mm of rainfall above normal, Boulder City, Nevada receiving 28.2 mm above normal and Yuma, Arizona (nearest reporting station to Glamis, California) receiving normal rainfall. Rainfall during March-May on the Jornada was more than 60 mm above average. The differences in mite faunas in the litter buried in these areas from mid-March through May undoubtedly reflect that rainfall.

It is also possible that the higher temperature in the Mojave, Sonoran and Coloradan deserts in addition to moist soils resulted in rapid decomposition of the creosotebush litter. Santos and Whitford (unpublished data) have shown a succession in soil microarthropods associated with the degree of organic matter breakdown. The litter communities in the other hot deserts with the large numbers of psocoptera are similar to communities found in litter buried in the Chihuahuan desert for 90 days in the summer. Many of these questions will be answered when more complete data are available in a comparison of the hot deserts.

The data presented and discussed here allow us to produce a tentative picture of the trophic relationships and dynamics of desert litter processors (Figure 1). Where present, subterranean termites probably process a significant proportion of standing dead annuals and grasses as well as the fecal material from cattle and lagamorphs. The relative amounts and types of litter consumed require study in other deserts. When termites harvest material from the surface that material is translocated to some as yet undetermined depth in the soil where it is converted to termite biomass. The depth and location of termite colonies in the desert soil thus determine where these energy and nutrient sinks are located. Returns to the shallow soil occur via predation on termite workers by lizards and ants and by death of alates. We know very little about the size of these fluxes and although we are currently studying them, it will be several years before we can make an accurate assessment of the role of termites in decomposition and nutrient release in desert ecosystems.

The processing of leaf litter on the soil surface is also not well understood. We know that organic matter loss from surface litter occurs at rates similar to that of buried litter for the same time periods and that during wet periods there is a complex mite fauna in the surface litter. Also we have recent evidence that nematodes are present in dry mixed creosotebush litter (unpublished observations in collaboration with D. Freckman). We hypothesize that the processing of surface litter is the same as buried litter (Figure 1) and that there are diel migrations of mites and nematodes into and out of the litter dependent upon moisture conditions in the litter and soil. Studies are in progress to examine these relationships.

The processing of buried litter and annual roots is the most completely studied part of the system (Figure 1). Our data indicate that the initial decomposition (organic matter loss) is due to bacterial activity. Although fungi are present the fungi do not appear to be contributing very much to initial CO_2 production and organic matter breakdown. Protozoans and bacteriophagic nematodes enter buried litter and establish large populations within a few days after litter is buried. The populations of nematodes are initially controlled by tydeid mites. After approximately 30% of the original organic matter has disappeared, fungivorous tarsonemid and/or pyemotid mites begin grazing on the fungi and fungivorous nematode populations increase. In later stages of decomposition predatory Gamasina mite populations increase and they reduce the grazing mite populations as well as the free living nematodes. In late stages of decomposition, psocopterans and collembolans make up a substantial part of the leaf litter community (Figure 1). We have no data on the trophic relationships of psocopterans and collembolans in desert litter communities.

The limited data from the other North American hot deserts suggests many similarities in the litter community structure and processing of dead plant material. We expect the similarities to be great and for the differences to be instructive.

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ACKNOWLEDGEMENTS

This research was supported by Grant DEB-77-16633 from the National Science Foundation.

APPENDIX I.

List of scientific names of plants and families of arthropods.

Plants

Cercidium microphyllum (Torreynum)
Cereus giganteus (Engelman)
Encelia farinosa (Gray)
Flourensia cernua (DC.)
Gutierrezia spp. (Britton and Rusby)
Larrea tridentata (Coville)
Olneya tesota (Gray)
Yucca schottii (Engelman)

Arthropods

Acari

- Bdellidae (Duges)
- Cunaxidae (Thor)
- Laelapidae (Berlese)
- Nanorchestidae (Grandjean)
- Oribatid (Duges)
- Pyemotidae (Oudemans)
- Raphignathidae (Kramer)
- Rhodacaridae (Oudemans)
- Smarididae ((Kramer)
- Tarsonemidae (Kramer)
- Tetranychidae (Donnadieu)
- Tydeidae (Kramer)

Insecta

- Isoptera
  - *Gnathamitermes tubiformans* (Buckley)
- Psocoptera
  - Liposcelidae
  - Trogiidae

SOIL ANIMAL SPECIES DIVERSITY IN A SEPARATED DUNE GRASSLAND ECOSYSTEM

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INTRODUCTION

Faunal investigations of isolated dune biotopes provide much important information for rational management of natural resources. They ensure a better analysis of the fauna-floristic complexity and the regulation mechanism of ecosystems productivity.

The purpose of the present investigation was the analysis of:

1) horizontal and vertical distribution of soil fauna depending on its directional exposure and the height of a grey dune,
2) quantitative and qualitative changes of the developmental forms (larvae and pupae) of soil entomofauna,
3) the structure of dominance and species density of soil fauna in the isolated dune ecosystem.

METHODS

The investigations in June and July 1976 - 1978 followed preliminary observations in 1975. Soil sampling after Ghilarov 1965 was the method applied here and 144 samples each 0,5 x 0,5 m by 30 cm deep including the vertical distribution of 0-10, 10-20 and 20-30 cm were collected.

The isolated dune biotope studied is one of the highest (50 m altitude) in the Czołpińskie Dunes situated in Słowiński National Park. The flora of this biotope represented a typical complex of grey dunes called Elymo-Ammophiletum Festucetosum arenariae by Wojterski (1964).

Twelve investigation sites were set up in this ecosystem, 3 each to analyse the north, south, east, and west sides of the dune; also the foot, the middle and the top of the isolated dune biotope were sampled.

RESULTS

No marked differences among the soil faunal communities of isolated dune biotope were observed in the respective years. Among animal communities coexisting in sandy dune soil the Coleoptera (95%) dominated over the Lepidoptera (3%) and Diptera (2%) (Figure 1).

Among developmental forms of soil entomofauna imagines comprising (81%), *Malachius aeneus* L., *Philopedon plagiatus* Schall. and *Aegialia arenaria* Fbr. dominated over the larval forms (11%) *Anomala aenea* Deg. *P. plagiatus*, *Polyphylla fullo* L. and pupal forms (8%) *A. aenea*, *P. plagiatus* forms.

Vertical distribution analysis showed that 81% of soil fauna was found in 0-10 cm, 17% in 10-20 cm and 2% in 20-30 cm samples (Figure 1). *Malachius aeneus*, *P. plagiatus* and *Coccinella septempunctata* L. were the dominant species in the 0-10 cm samples, while *P. plagiatus*, *A. aenea* and *A. arenaria* in the 10-20 cm samples and *P. plagiatus* and *A. aenea* in 20-30 cm strata.

Soil fauna was concentrated mostly at the foot of the dune biotope (81%), fewer in the middle (11%) and the least at the top (8%) (Figure 2). At the foot of the dune such species as *P. plagiatus*, *C. septempunctata* and *A. arenaria* were predominant whereas *M. aeneus* and *P. plagiatus* in the middle, and *M. aeneus*, *A. arenaria* at the top.

Summing up, the species composition of the following soil fauna, *P. plagiatus* (21%), *Malachius aeneus* (17%), *A. arenaria* (14%), *C. septempunctata* (12%), *A. aenea* (9%) and *Demetrias monostigma* Sam. (5%), were the predominant species (over 5% dominance). These species were found most often in the south side of the dune (38%), less in the east (33%) and the least in the west (18%) and north (11%) (Figure 3).

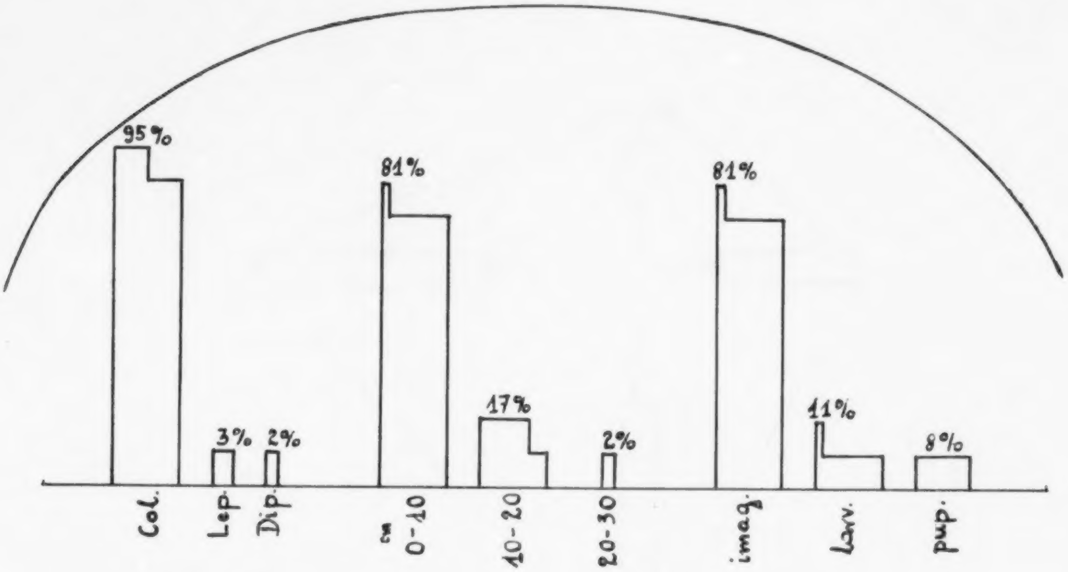

Figure 1: CONCENTRATION OF SOIL FAUNA, VERTICAL DISTRIBUTION AND DEVELOPMENTAL FORMS OF SOIL FAUNA IN ISOLATED DUNE ECOSYSTEM.

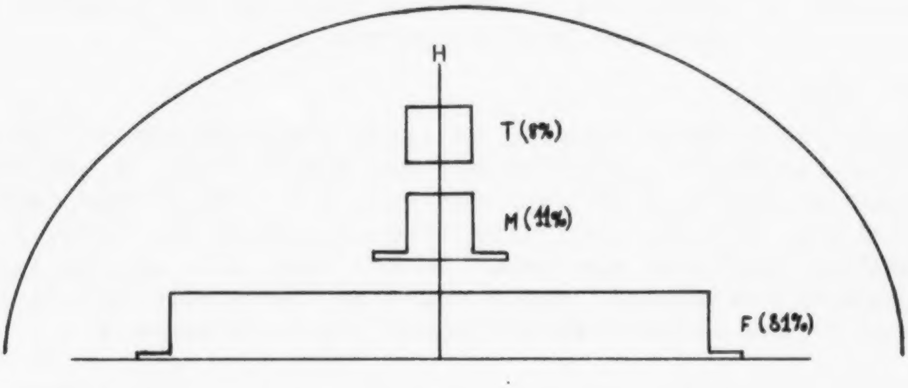

Figure 2: CONCENTRATION OF SOIL FAUNA AT THE FOOT (F), IN THE MIDDLE (M) AND AT THE TOP (T) OF AN ISOLATED DUNE BIOTOPE (%).

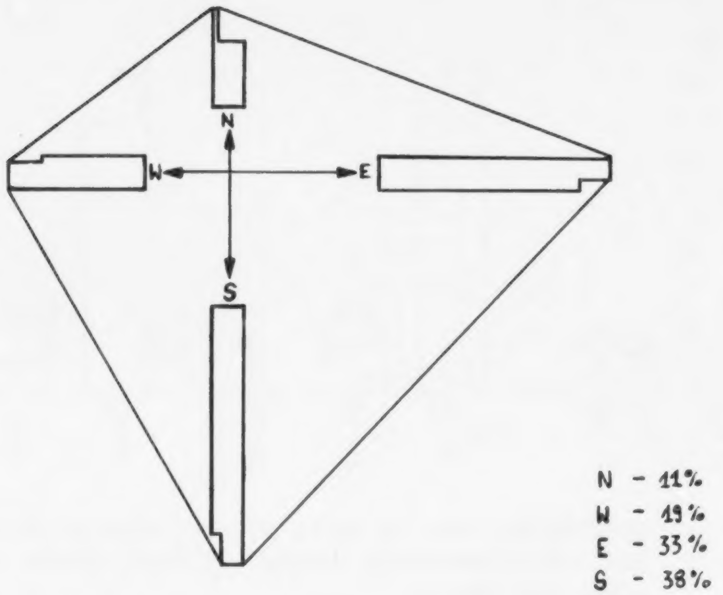

Figure 3: DISTRIBUTION OF SOIL FAUNA ON THE SIDES OF THE ISOLATED DUNE ECOSYSTEM (%).

Soil fauna density analysis (individuals/m^2) showed that the density coefficient was the highest, 9, on the south side at the foot of dune biotope, 8 in the middle, and 4 at the top. On the east side likewise, 9 at the foot, 5 in the middle, and 5 at the top. On the west side at the foot the density coefficient was 6 and 2 in the middle and at the top, and on the north 2 at all three levels (Figure 4).

Varied species dominance was distinguished when analysing the directional sides of the dune. Philopedon plagiatus was dominant on the south, A. aenea on the east, A. Arenaria and C. septempunctata on the north, and A. arenaria on the west side.

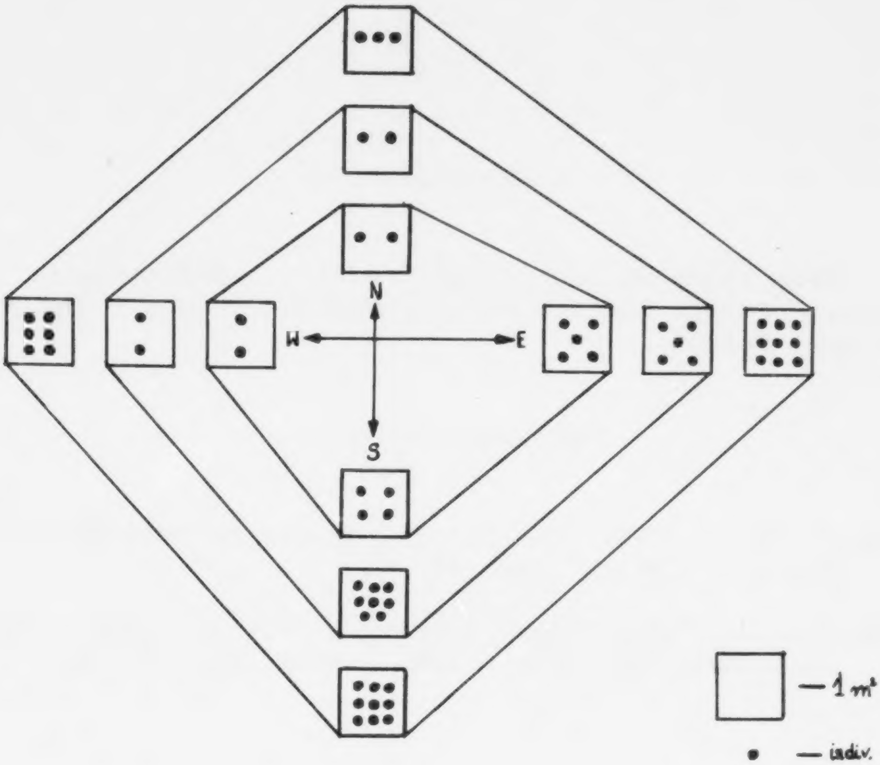

Figure 4: DENSITY COEFFICIENT ON DUNE SIDES AT THE FOOT, IN THE MIDDLE AND AT THE TOP OF ISOLATED DUNE ECOSYSTEM (individuals/m^2).

RECAPITULATION

The investigation gave information about faunal communities in sandy soil of a isolated dune grassland ecosystem (Elymo-Ammophiletum). Coleoptera prevailed among soil faunal communities (95%). Fauna was concentrated mostly in soil 0-10 cm deep, particularly on the south and east sides at the foot of the isolated dune ecosystem. On the south side of dune biotope, Philopedon plagiatus was the predominant species whereas Anomala aenea on the east side, Aegialia arenaria on the west and A. arenaria and C. septempunctata were dominant on the north side.

The above mentioned faunal communities are determined by weather conditions such as winds, air-temperature and insolation. In spite of dominance of phytophages (51%) no deleterious influence dangerous to fauna of isolated dune ecosystem has been observed so far.

ACKNOWLEDGMENTS

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DIVERSITY TRENDS AMONG THE INVERTEBRATE LITTER DECOMPOSERS OF A SUBALPINE SPRUCE-FIR SERE: A TEST OF ODUM'S HYPOTHESES

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USA

In 1969 Eugene Odum propounded 24 attributes of ecosystems which, theoretically, undergo systematic change during succession. The attributes are grouped into the following categories: community energetics, community structure, life history, nutrient cycling, selection pressure and overall homeostasis. Most of the predicted trends are at least potentially testable, while a few are basically vague. To date the testable hypotheses have not been tested *en mass* on one ecosystem involving a straightforward succession. Further, no studies have addressed them in which essentially all higher taxa have been studied simultaneously. Clearly before Odum's hypotheses can form a basis for understanding successional trends of ecosystems, their validity must be determined. Preliminary results of a study of invertebrate litter decomposers reported here represent part of a large-scale effort to test most of Odum's hypotheses simultaneously utilizing data on all important taxa present within a subalpine spruce-fir successional sequence.

MATERIALS AND METHODS

The study area was located in the Wasatch Mountains of northern Utah, U.S.A., at elevations between 2550 m and 2600 m. Study plots were established atop an undissected plateau-like ridge of gentle topography. Further details of the area were discussed by Schimpf, Henderson and MacMahon (1980).

The successional sequence studied and believed to be a chronosequence (Schimpf et al., 1980), began with herb-dominated meadows which were invaded by quaking aspen (*Populus tremuloides*). The latter were, in turn, invaded and replaced by subalpine fir (*Abies lasiocarpa*) which was succeeded by Engelmann spruce (*Picea engelmannii*). A mixed spruce-fir forest was the apparent local climax.

Three replicate seres were selected for detailed study. Within each sere, plots measuring 20 m by 25 m were established. Each plot was divided with twine into square meter areas. Each square meter from which samples were taken was selected from coordinates generated by a computer-run, random numbers program. Numbers were generated without replacement so that no square meter was sampled more than once. During the summer the three replicates were sampled on a 3-week rotation. Two of the replicate seres were sampled only during snow-free conditions. One, designated Cattle Guard, was also sampled during winter at 3-week intervals for the moderate snow depths (1.5 m) which prevailed during the time interval herein reported. The present report spans the dates from 4 August 1976 to 16 August 1977. It must be noted that after 11 November 1976, analyses of all sample periods for which samples were collected were not available.

Samples were collected with a hand-operated, garden-type coring device with a cross-sectional area of 38 cm^2. Cores extended through the litter layer, if present, and 5 cm into the mineral soil. The litter portion was removed by hand and placed in a plastic bag. The remaining soil was placed in a separate bag. Four cores were collected from the centers of the 4 quadrates composing the square meter. All litter thus collected from a square meter was placed in a single bag and mixed. The soil was treated similarly. For a given sample date, within each seral stage 5 square meters were sampled. Since the meadows lacked litter, a given sample date is represented by 35 samples. The samples were returned to the laboratory and processed immediately.

The samples were first weighed and weighed subportions removed for extraction of nematodes. The remainder was used for extraction of arthropods. Nematodes were extracted by a technique essentially identical to that of Uhlig (1966, 1968). Other procedures, based on flotation of the nematodes on various solutions, were tried but were found to be ineffective for samples containing appreciable quantities of litter. Arthropods were extracted using Tullgren funnels. Extractions were analyzed by assigning individual organisms to an "operating taxonomic unit" or species and making counts within each such unit. This procedure was necessary due to the apparent abundance of undescribed taxa. The data were stored on magnetic tape for subsequent computer analysis. For the present preliminary analysis, data for the litter and soil portions of each sample were combined. For each seral stage for each date, and separately for nematodes and arthropods, the total number of species, the Shannon-Wiener index of diversity (H') and the index of equitability (J) were calculated. The results are presented graphically in figures 1-6.

RESULTS AND DISCUSSION

Odum's hypotheses eight and nine, respectively, predict that species diversity (variety component) and species diversity (equitability component) should proceed from low to high across succession. The variety component itself is here resolved into two components:

total number of species (species richness) and H', the Shannon-Wiener information diversity index. For nematodes, the species richness (figure 1) in the meadows ranged between 6 and 22 and, except for a slight overlap on two dates, is clearly less than in the other seral stages. Species richness in the aspen, fir and spruce were similar and ranged between 26 and 45. For some dates the number were rather different; however, from one date to another the tree stage with maximum, intermediate and minimum numbers of species changed. The Shannon-Wiener index for nematodes (figure 2) varied from 0.7 to 1.3 and generally reveals no clear-cut differences between the seral stages, except possibly that the value for the meadows was somewhat less. The order of seral stages with maximum to minimum clearly changed from date to date. The index of equitability, J, (figure 3), ranged from 0.56 to 0.95. Again, no clear trends were evident with the seral stage order of maximum to minimum J varying across the sample dates.

Species richness for the arthropods (figure 4) varied between 1 and 54. Values in the meadows were consistently less than in other stages for the same date and did not overlap with them. In the aspen, fir and spruce stages the numbers were higher with the stage order of maximum to minimum varying from date to date. H' (figure 5) varied from 0.2 to 1.4 with values in the meadows generally lower than in the other seral stages and much more erratic. Values in the tree stages were higher and less erratic. Further, the order of maximum to minimum values in the tree stages varied across the sampling dates. Equitability, J, ranged between 0.0 and 1.0. The values were highly erratic in the meadows; otherwise no clear-cut trends were evident. The seral stage order of maximum to minimum values for all four stages changed across sample dates.

Species richness for both nematodes and arthropods (figures 1 and 4) were generally lower for the meadows; however, no successional pattern was evident for the aspen, fir and spruce stages. The values of H' (figures 2 and 5) were somewhat lower in the meadows with no emergent pattern in the tree stages. These results appear to contradict Odum's hypothesis concerning the variety component of diversity. The values of the equitability component, J, (figures 3 and 6) for both nematodes and arthropods revealed no clear successional trends. Therefore, these data seem to contradict Odum's hypothesis relating to the equitability component of diversity. For these preliminary analyses great caution must be exercised in reaching any firm conclusions. Subsequent calculations will be performed on the separate soil and litter faunas. Further, the effects of varying litter amounts among the actual sites sampled, water content, temperature and season will be assessed. It is possible that these more detailed analyses will reveal more clear-cut trends with which to test Odum's hypotheses.

FIGURE 1. Species richness for nematodes.

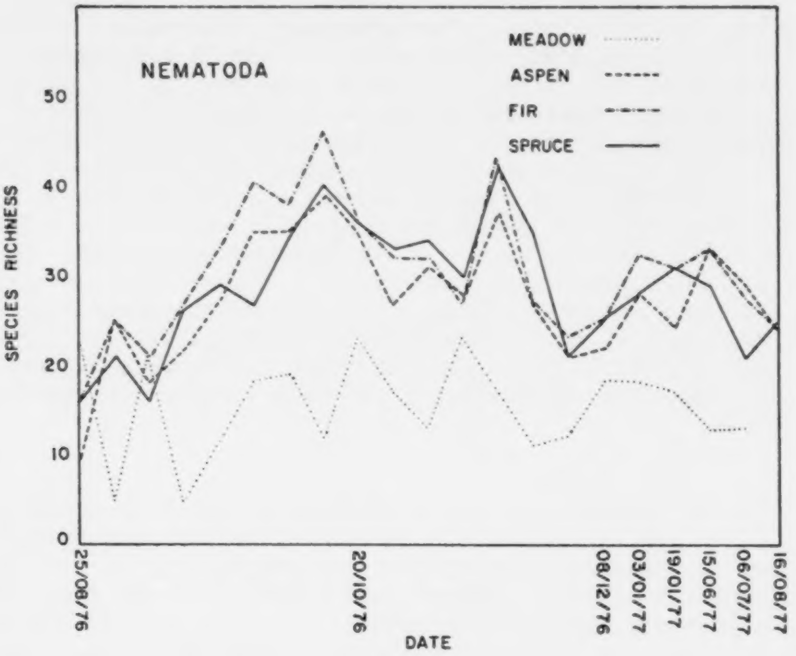


FIGURE 2. Shannon-Wiener diversity index (H') for nematodes.

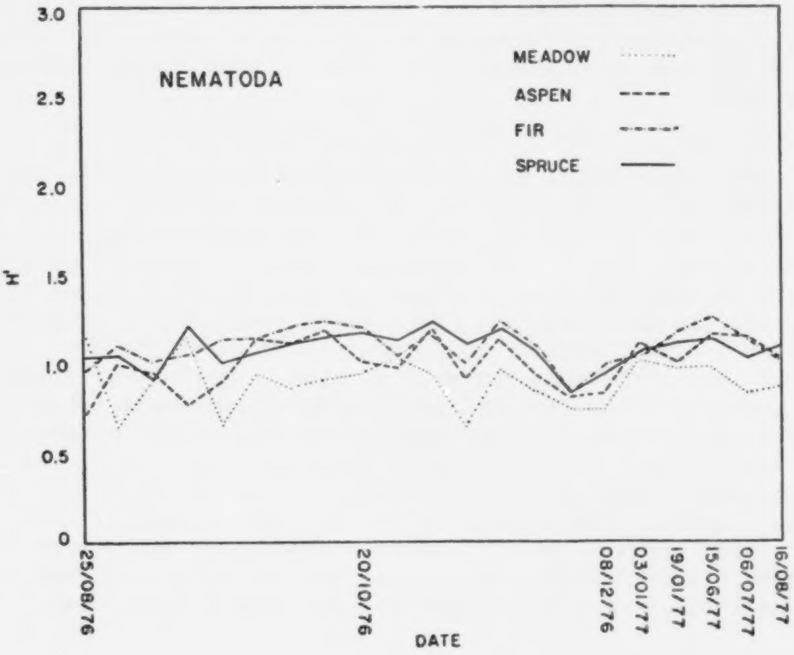
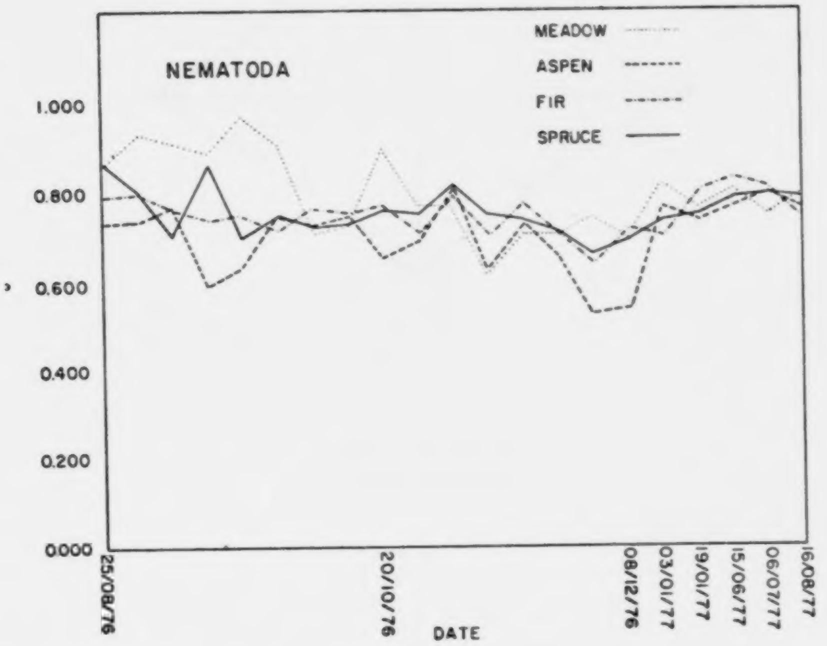
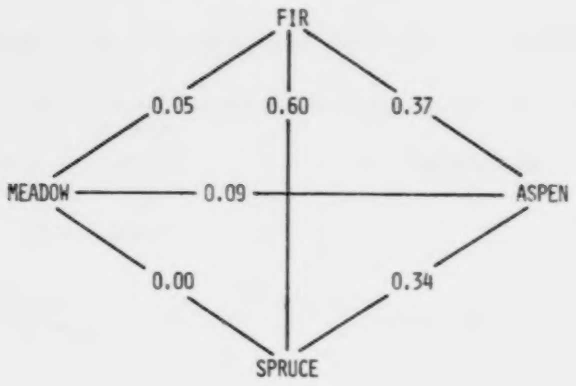


FIGURE 3. Equitability index, J, for nematodes.



JACCARD COEFFICIENTS
NEMATODA, JANUARY


FIR
0.05
0.60
0.37
MEADOW
0.09
ASPEN
0.00
0.34
SPRUCE

JACCARD COEFFICIENTS
ARTHROPODA, FEBRUARY

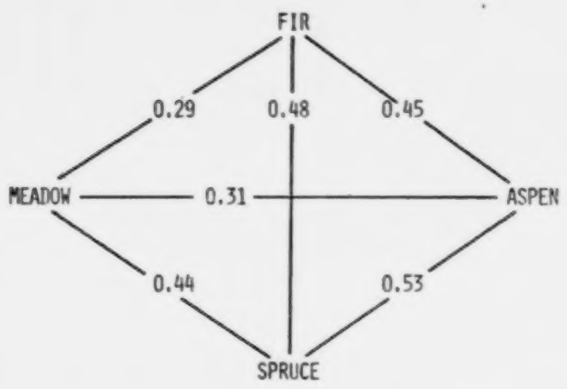

FIR
0.29
0.48
0.45
MEADOW
0.31
ASPEN
0.44
0.53
SPRUCE

FIGURE 4. Species richness for arthropods.

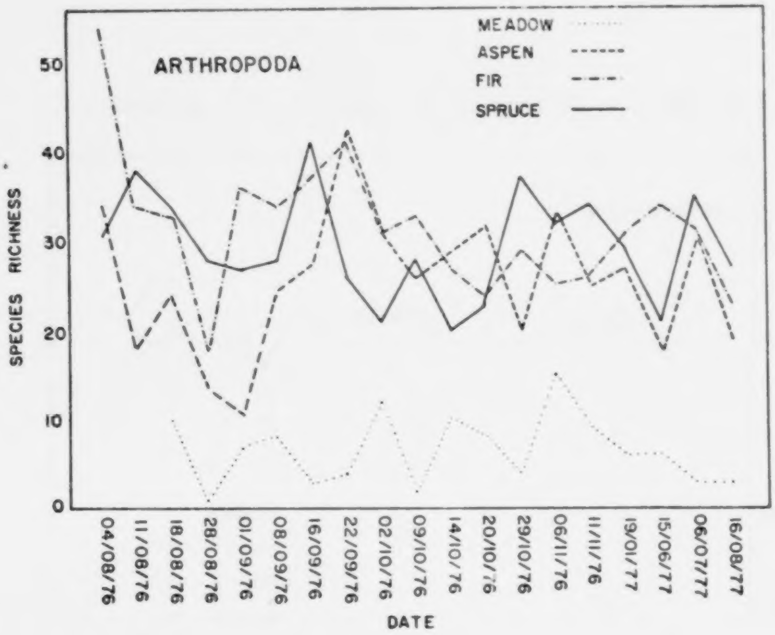


FIGURE 5. Shannon-Wiener diversity index (H') for arthropods.

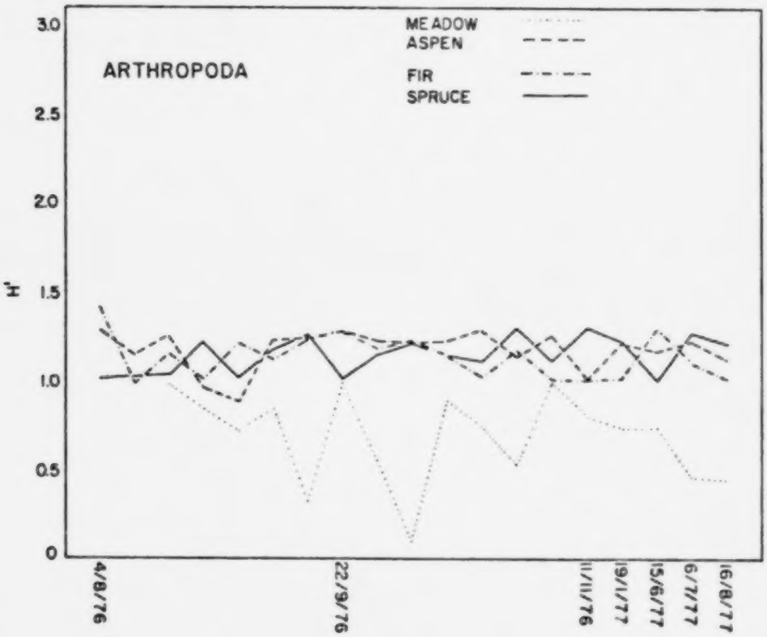
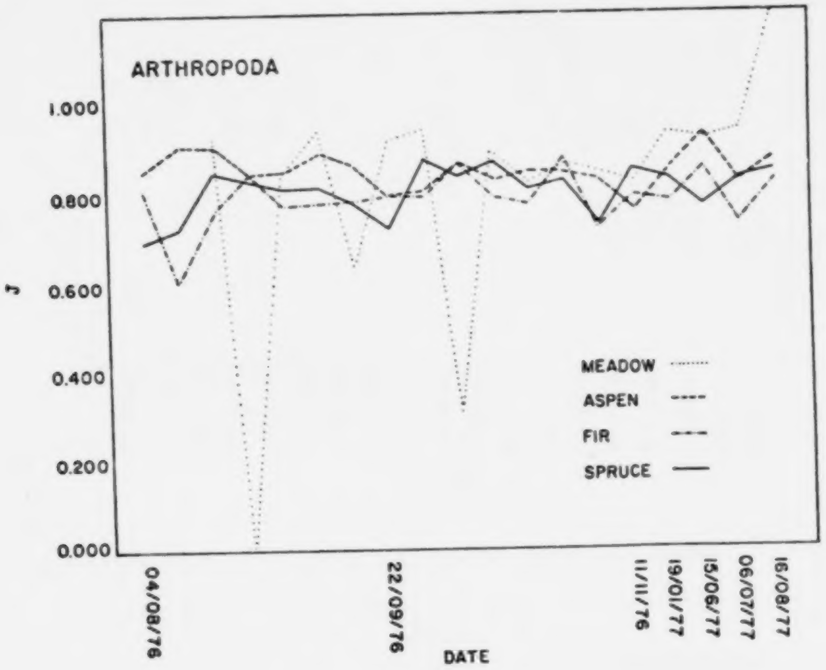


FIGURE 6. Equitability index, J, for arthropods.



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QUESTIONS and COMMENTS

J. CURRY: Could you comment on the biological significance of H' as a measure of diversity in view of the rather anomalous results it appears to give in your data when the meadow community is compared with those in the spruce-fir sites?

L.W. BENNETT: H', an information index of diversity, is not especially intuitive in a biological sense. It requires much more thought to make an adequate response.

J.A. ADDISON: Were all your sites at the same elevation or were you looking at changes along an elevational gradient?

L.W. BENNETT: All sampling sites were within ca. 100 m of 2,500 m elevation.

D. FRECKMAN: Sample size? determination of extraction efficiency? Does your method select for certain TG? What does TG (community structure) look like?

L.W. BENNETT: Sample size: ca. 38 cm^2 of soil to a depth of 5 cm and through whatever depth of litter. Samples were taken from 5 randomly chosen square meters from each seral stage on a 3 week rotation. Extraction efficiency: Rough estimates at present suggest approximately a 75% efficiency for most nematode groups using the Uhlig method. (Community structure will be discussed in subsequent papers).

B. STEVENSON: It would seem to me that changes in the components of H' (equitability and richness) would vary annually due to organic matter decomposition. Did you analyse and/or control for these changes?

L.W. BENNETT: Data for such analyses were collected but have not yet been fed to the computer! They will be very soon.

V. HUHTA: I can give some additional information. We have investigated the effects of clear-cutting on soil animal communities in Finland. Coleoptera and Araneae were identified. After clear-cutting, the diversity in the spider community was increasing in southern Finland but decreasing in northern Finland. The diversity of the coleopteran community was decreasing in southern Finalnd but increasing in northern Finland. No conclusions could be made.

L.W. BENNETT: It is quite possible that species richness for a given taxocene may increase or decrease depending on local conditions and the species available for colonization.

SYNECOLOGY OF FOREST SOIL ORIBATID MITES OF BELGIUM.
I. THE ZOOSOCIOLOGICAL CLASSES.

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Belgium

This article is the first part of a synecological analysis carried out on thirty taxocenoses of Oribatid mites living in the organic horizons of the soils of deciduous forests in Belgium.

Any synecological analysis requires, first of all, representative and sufficient information about the physiognomical structure of the taxocenoses. The first chapter of this article shows how we got the information and how we presented it in the form of zoosociological relevés.
Then, any synecological step includes the delimitation of relevés groups which have the same zoological composition and form zoosociological classes. Finally, a list of species results from this collection of relevés. These species are influenced by the same environment and define an original combination of species which forms an ecological group (GOUNOT, 1969).

The second chapter of this article deals with the delimitation of the zoosociological classes of relevés.

CHAPTER 1. - THE RELEVÉS.

1. The biogeocenoses.

Before beginning the analysis, we decided to choose sites which were comparatively undamaged and not very influenced by man. These sites we have chosen tend to show the diversity of the deciduous vegetation of Belgium. In this way, our conclusions will be generalized to the whole taxocenoses of Oribatids of the organic horizons of deciduous vegetation of the country.

As the figure 1 shows it, the organic horizons we have met can be divided into four principal types according to their morphological structure and a few physico-chemical characteristics considered to be significant (KUBIËNA, 1950 and DELECOUR, 1978).

The organic horizons with calcic mull are found on calcareous outcrops or chalks. The soils where they are found always have a good chemical fertility and undergo a long period of drought in summer. The studied calcicole vegetations, all of them being medio-european climax beechwoods of the Fagion, are located in Thynes (nr. 1 ; plateau of the Condroz ; 160 m), Rémersdael (2 ; Entre-Vesdre-et-Meuse ; 215 m), Crupet (3 ; Condroz ; 196 m), Dourbes (4 ; Famenne ; 160 m) and Marche-les-Dames (5 ; Meuse trench ; 120 m).

The organic horizons with non-calcic mull such as those with moder-mor can be found on soils presenting a wide range of fertility and moisture conditions. However, the decomposition processes (in the widest sense) of the organic matter are more rapid for the first ones than for the second ones, for there is a Fm horizon, in the BABEL's meaning (1971).
Some vegetations are climax phytocenoses of the Fagion and Quercion. The first ones are situated in Marneffe (9 ; Hesbaye ; 169 m), Mont-St-Aubert (11 ; hainault loessic region ; 88 m), Houyet (13 ; Famenne ; 244 m), Bohan (14 ; southern Ardenne ; 315 m), Annevoie (15 ; Condroz ; 246 m), Fouron-St-Martin (21 ; Entre-Vesdre-et-Meuse ; 250 m), Eupen (22 ; Hertogenwald, northern Ardenne ; 420 m). The second ones have been found in

Figure 1. - Grouping of sites according to the humus category, the pedological class, fertility and the hydrous nature of the soil. Mention of the phytosociological and chorological position of their phytocenosis. — Pedological class : C, calcimagnesic ; H, hydromorphic ; B, brown ; ND, not very developed ; PB, podzolic brown ; P, peat. — Hydrous evaluation : GD, good internal draining ; DD, deficient internal draining ; F, fluctuating hydrous conditions ; M, moist. — Phytosociology : F, Fagion ; C, Carpinion ; FC, Fraxinio-Carpinion ; Q, Quercion ; A, Alnion glutinosae ; V, Vaccinio-piceion. — Chorology : A, association of the atlantic province ; M, association of the medio-european province.

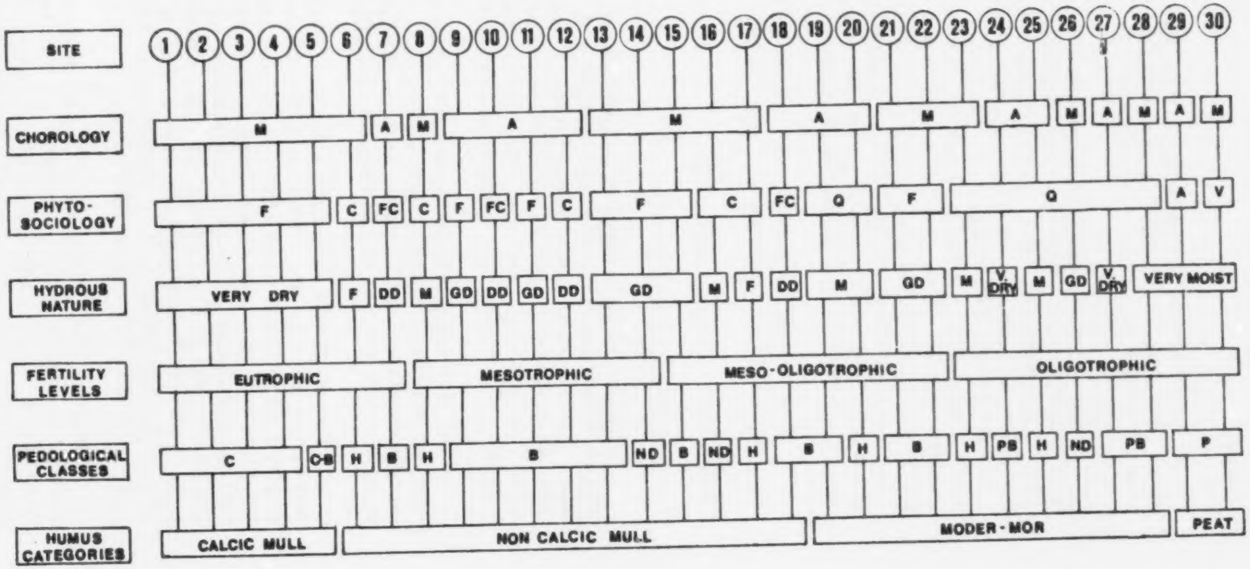
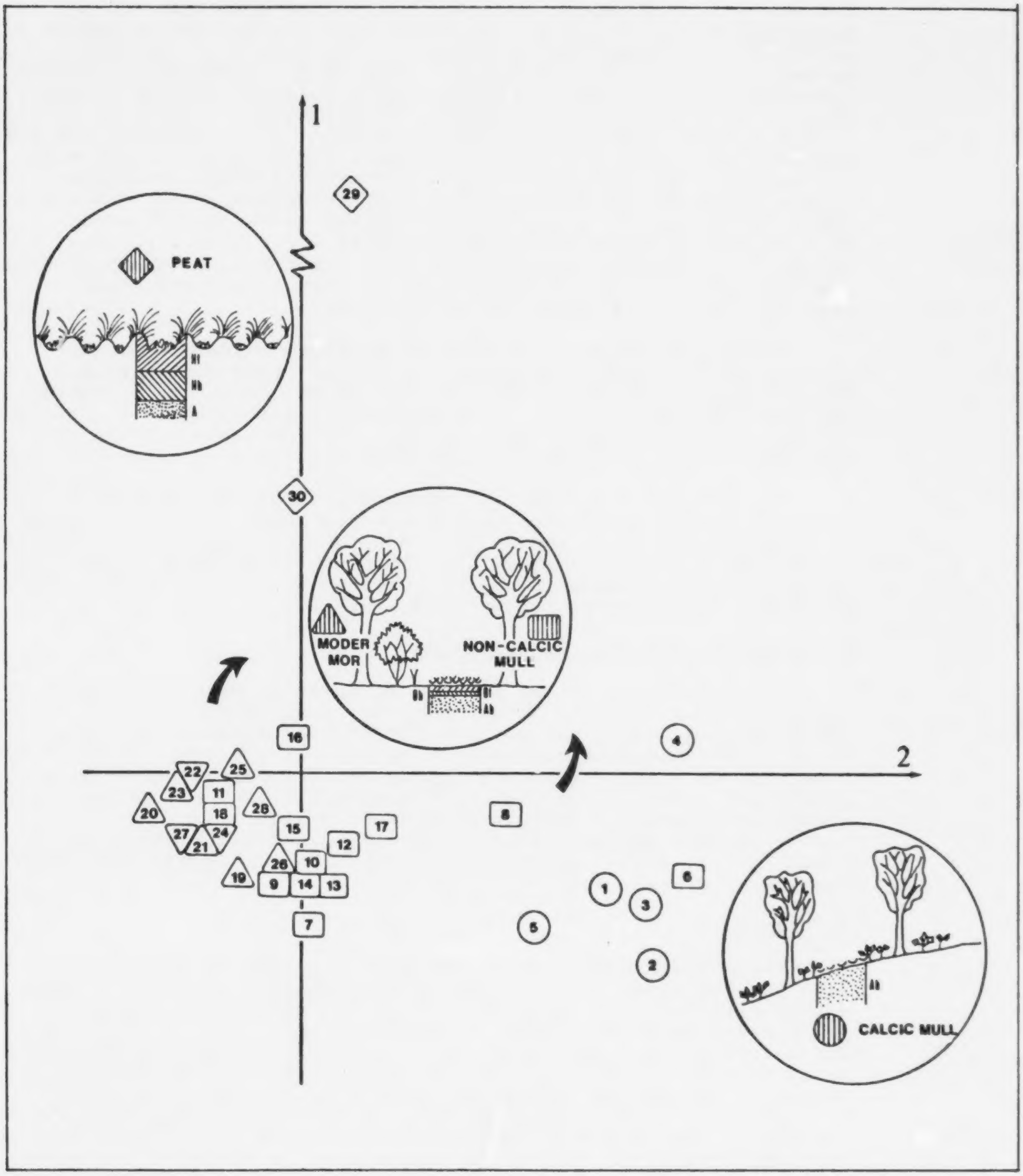

SITE
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
CHOROLOGY
M A M A M A M A M A M A M
PHYTO-SOCIOLOGY
F C FC C F FC F C F C FC Q F Q A V
HYDROUS NATURE
VERY DRY F DD M GD DD GD DD GD M F DD M GD M V. DRY M GD V. DRY VERY MOIST
FERTILITY LEVELS
EUTROPHIC MESOTROPHIC MESO-OLIGOTROPHIC OLIGOTROPHIC
PEDOLOGICAL CLASSES
C C-B H B H B ND B ND H B H B H PB H ND PB P
HUMUS CATEGORIES
CALCIC MULL NON CALCIC MULL MODER-MOR PEAT

Figure 2. - Reciprocal averaging of 30 relevés out of 357 ecological species of hemedaphic Oribatids. Plan of the axes 1 and 2. — The numbers indicate the origin of the relevés. — The categories of humus are designated by a symbol.



Cul-des-Sarts (23 ; southern Ardenne ; 359 m), Ham-sur-Heure (24 ; hainault alluvial region ; 177 m), Angleur (26 ; Condroz ; 170 m), Ruien (27 ; coarse-loamy Flanders ; 127 m). The other vegetations are edaphic climax and fall into the Carpinion or the Quercion. The first ones are located in Habay-la-Vieille (6 ; Lorraine ; 303 m), Arquennes (7 ; brabant loessic region ; 107 m), Froidchapelle (8 ; Fagne of the Entre-Sambre-et-Meuse ; 235 m), Angre (10 ; hainault loessic region ; 88 m), Tarciennes (12 ; brabant loessic region ; 230 m), Sadzot (16 ; western Ardenne ; 370 m), Waillet (17 ; Famenne ; 228 m), Eugies (18 ; hainault loessic region ; 138 m). The second ones can be found in Grand-Leez (19 ; Hesbaye ; 173 m), Houthulst (20 ; coarse-loamy Flanders ; 15 m), Courrière (25 ; Condroz ; 267 m), Eupen (28 ; Brachkopf, northern Ardenne ; 545 m). In this last biogeocenosis, the humus is a peculiar mor : the thickness of the organic horizons does not exceed 5 cm and moreover, the C/N ratio is rather weak (± 16), this is why the humus of this site bears a resemblance to the moder.

The two peat organic horizons we have met belong to biogeocenoses whose botanical composition offers great differences. This is due to the fact that the site of Malempré (29 ; central Ardenne ; 425 m) is full of ferruginous water streamlets whereas in the site of Roumont (30 ; central Ardenne ; 411 m) the surface horizons of the soil are only fed with the water of rains and snow.

Let us point out that two phytocenoses are enclaves of atlantic groups in the medio-european province. The phytocenoses in question are nr. 25 and nr. 29. In both cases, particular edaphic conditions (moist and gleyified limon on the surface in the site nr. 25 ; permanent runnels on the surface in the site nr. 29) can prove the transgressions (SOUGNEZ, 1974).

2. Ecological species of Oribatids.

The definition of the systematic units we have retained, units which we think to be the smallest taxonomical entities presenting an ecological unity (TUFFERY & VERNEAUX, 1968), is based on the neotenic concept of the Acarida developed by GRANDJEAN (1938). We associate to the phylogenetic independence between adults and immatures proved by this author (1947 a) an ecological independence pointed out by TRAVÉ (1964).
Larvae, nymphs and adults are full ecological species,and we assign a distinct zoosociological part to them. There are 357 ecological species of Oribatids.

3. Sampling.

The relevés constituting has been realized in accordance with the " petites faunes " method of GRANDJEAN (1947 b). This method advocates the concentration of the collecting places in small areas which have been chosen with care.
Our knowledge does not enable us to estimate the biotic homogeneity (GOUNOT, 1969) of any taxocenosis of Oribatids. This is why we decided to reduce the surface of the sampling areas to a minimum. In this way, we hoped to meet biotopes whose life conditions were not very heterogeneous (CANCELA DA FONSECA & VANNIER, 1969). In view of the dimensions of the Oribatid mites and the parcelling of the herbaceous tapetum of our forests, we decided the sampling area of each site to be a small area of

herbaceous vegetation typical of the phytocenosis.

In each sampling area, we have distinguished the taxocenoses of the " litter " habitats from those of the " humus " habitats. In the non-peaty forests, the " litter " habitat consists of surface holorganic layers including the Of_2 micro-layer if it exists. The " humus " habitat consists of the Oh or Ah surface micro-layers (± 1 cm thick) according to the humus categories. In peaty forests, we have chosen the Hf_1 layer as " litter " habitat and the surface part of the Hh horizon as " humus " habitat because these two horizons exhibit a morphological discontinuity state similar to the one observed between the " litter " and " humus " habitats of the other non-peaty biogeocenoses.

The sampling has been made in spring and in fall. We have chosen these two seasons for we observe a density forester optimum in summer and in spring for the " litter " habitats and in fall for the " humus " habitats (LEBRUN, 1964).

4. The three types of relevés.

On the whole, twenty samples have been taken in each area. The specific and numerical lists of these samples have been put together to form three relevés by biogeocenosis : a " litter " relevé, a " humus " relevé and a " hemiedaphic " relevé concerning the Oribatids living both in the " litter " and " humus " habitats. The " hemiedaphic " relevé is a kind of zoosociological reference standard since important variations of the morphology and of the physico-chemical composition of the forester organic horizons have been recorded. Thus, the " humus " habitat of a mull organic horizon is more mineral than the one of a moder organic horizon. Besides, the decomposition of the organic matter follows different biogeochemical processes according to the composition of the mineral sub-soil (TOUTAIN, 1974).

Since the relevés include much information, it will be easy to generalize the results deriving from their comparisons.

CHAPTER 2. - THE ZOOSOCIOLOGICAL CLASSES.

The zoosociological class concept is based here on the individualistic conception of the sociological categories (WHITTAKER, 1956) which recognizes the existence of the ecological continuum of the taxocenoses. This implies the approximate repetition (except for the uncertain variations) of the same specific combinations when the environment (in the widest sense) is about the same.
Consequently, the mesological similarity of the biotopes can be associated with the similarity of the specific and numerical profiles between the relevés. The purpose of this association is to determine the mesological frame which is necessary for the Oribatid ecological groups to develop and to remain.

1. Method.

The quantization of the similarities between the relevés has been realized with the help of the reciprocal averaging (BENZECRI & al., 1973). The similarity function is a distance, called χ^2 distance, which is determined from the conditional

frequencies on the specific numbers of individuals.
Then, the method describes the information put on the relevés table according to several linear orders by means of representations made of axes and points.
We think that those ordinations are of great ecological importance because the points corresponding to two relevés which have about the same distribution of individuals through the same species, mingle in the factorial hyperespace.
The algorithm which has been used is the one of LEBART & al. (1977).

2. The mesological frame.

The figure 2 shows the dispositions of the hemedaphic relevés-points in the space of the first two factorial axes. An assembly of relevés-points which refer to taxocenoses living in the moder-mor and non-calcic mull organic horizons focuses close to the center of gravity. The first axis is a segregation axis of the relevés-points dealing with the taxocenoses which develop in the peat organic horizons. The second axis is a segregation axis of the relevés-points indicating taxocenoses living in the organic horizons of soils with a high biogen elements content and, among others, calcic mull soils.

In relation to the third factorial axis (figure 3), the hemedaphic relevés-points are divided into two groups. The group on the left of the center of gravity is almost totally made of relevés-points relating to taxocenoses located in the north of the Sambre-Meuse trench while the other group consists of relevés points relating to taxocenoses situated in the south of this trench. In fact, the third axis seems to prove (except for points 2, 3, 24 and 25) that there is an excellent chorological parallelism between the taxocenoses of Oribatids and the phytocenoses sheltering them.

The fourth and following axes could not be interpreted on account of the ecological parameters we analysed.

The ordination of the hemedaphic relevés-points which we have just described is about the same than the one of the " litter " relevés-points alone or the " humus " relevés-points alone, according to the directions defined by the factorial axes nr. 1 and 2. In accordance with the direction of the third axis, the same macroclimatic antagonism can only be found with the analysis of the " litter " relevés-points. In the case of the " humus " relevés-points, this antagonism is present for all the points except for those indicating the moder-mor organic horizons.
Nevertheless, the convergence of the results of the three reciprocal averagings is undeniable.
Therefore, we come to the conclusion that, generally, there is an excellent physiognomical identity between the taxocenoses of the " litter " habitats and the ones of the " humus " habitats. Indeed, the exclusive (LEBRUN, 1971) or indifferent (LIONS, 1972) species are very few. Futhermore, our results state precisely the existence of an identical mesological frame which has an influence on the specific combinations of the " litter " and " humus " habitats. This frame consists of two components : the first one is an edaphic component which reveals the influence of the category of humus, this is to say the morphological and physico-chemical organization of the organic horizons on the

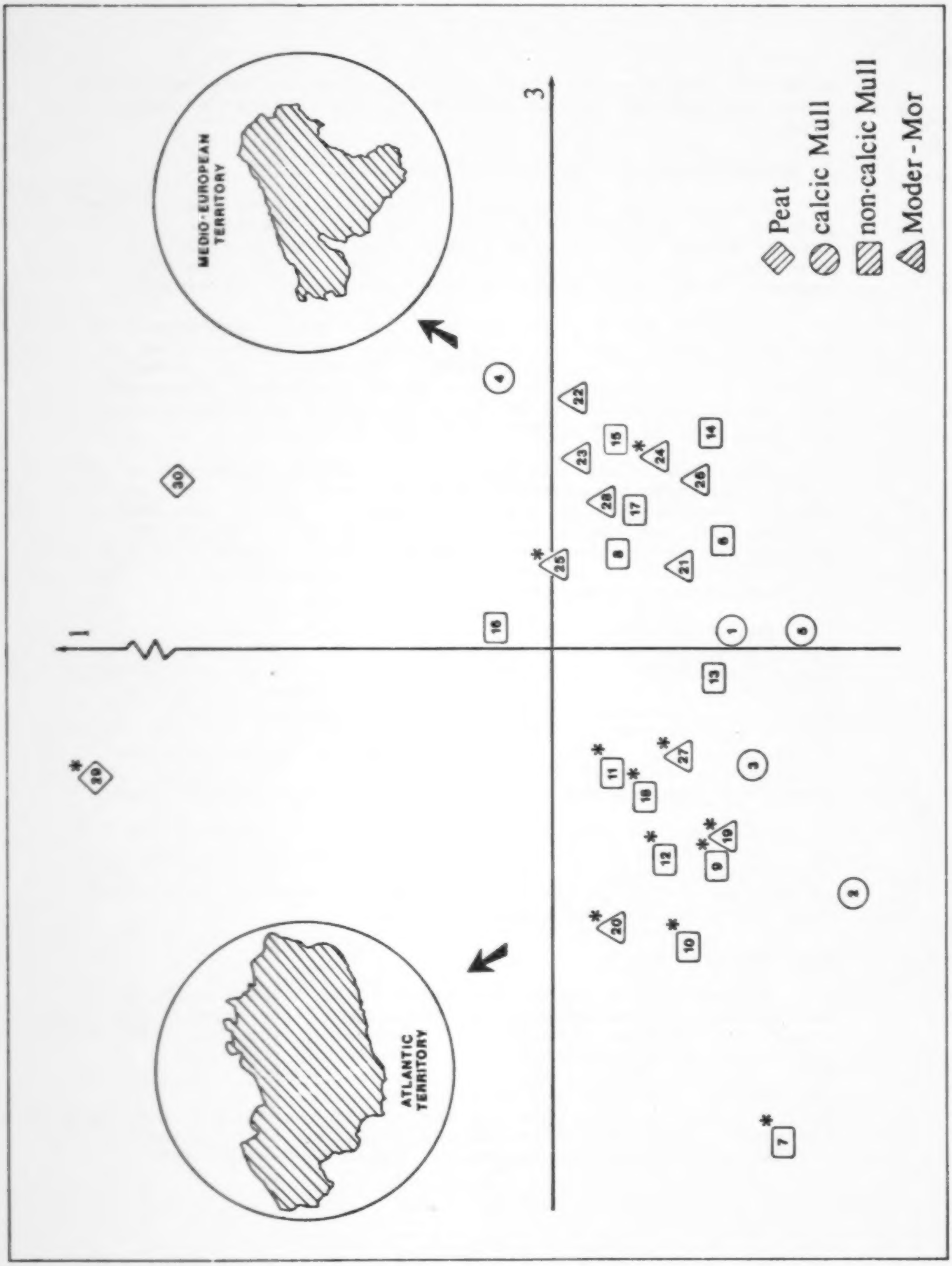


Figure 3. - Reciprocal averaging. Distribution of the 30 hemiedaphic relevés in the plan of the axes 1 and 3. — The asterisks mark the relevés indicating taxocenoses of sites whose phytocenosis is an association of the atlantic province. — Legend identical with figure 2.

Oribatid groups ; the other one is a climatic component which shows the influence of the climate of the atlantic or subatlantic type.

3. Delimitation of the zoosociological classes.

With the help of the natural subdivisions of the two components, we can define six homogeneous sub-assemblies of relevés, this is to say dealing with taxocenoses whose species seem to have about the same reaction towards the incriminated ecological factors. Those sub-assemblies form zoosociological classes.

As the figure 4 shows it, the first class corresponds to the sub-assembly made of the two relevés-points referring to the taxocenoses of the peat organic horizons. Thus, these taxocenoses can be found in biotopes which are almost permanently wet. The action of water on the taxocenoses of Oribatid mites has been pointed out by KNÜLLE (1957).

The second class consists of the relevés referring to the organic horizons taxocenoses of calcic mull soils where calcium takes a leading part in the biogeochemical cycles. The direct influence of calcium on the Oribatids has not been proved. However, since the quantity of ectoskeletal calcium (GIST & CROSSLEY, 1975) is important, there is probably vital physiological needs for this ion.

The third class corresponds to the relevés established from the taxocenoses of the organic horizons of non-calcic mull soils. These taxocenoses have a great zoosociological plasticity since their physiognomy recalls the one of the taxocenoses found in calcic mull horizons, when they are in organic horizons of soils with a high biogen elements content. In soils with a low biogen elements content, their physiognomy recalls the physiognomy of the taxocenoses which develop in moder-mor organic horizons and from which the relevés form the fourth zoosociological class.

The last two classes deal with the climatic component : one of them consists of the relevés relating to the taxocenoses of the atlantic territory. Thus, it is subject to a climate which is less hard than in the subatlantic territory whose relevés form the sixth zoosociological class.

CONCLUSIONS.

The ecological connection between the deciduous phytocenoses and the taxocenoses of Oribatids of the organic horizons cannot be admitted. Indeed, the deciduous phytocenoses are mainly influenced by the climatic factors while the taxocenoses of Oribatids they shelter are above all condioned by the edaphic factors and, secondarily, by climatic factors.
Now, we still have to work out the specific composition of each ecological group and to reveal the relations between the groups, the two mesological components and other ecological data.

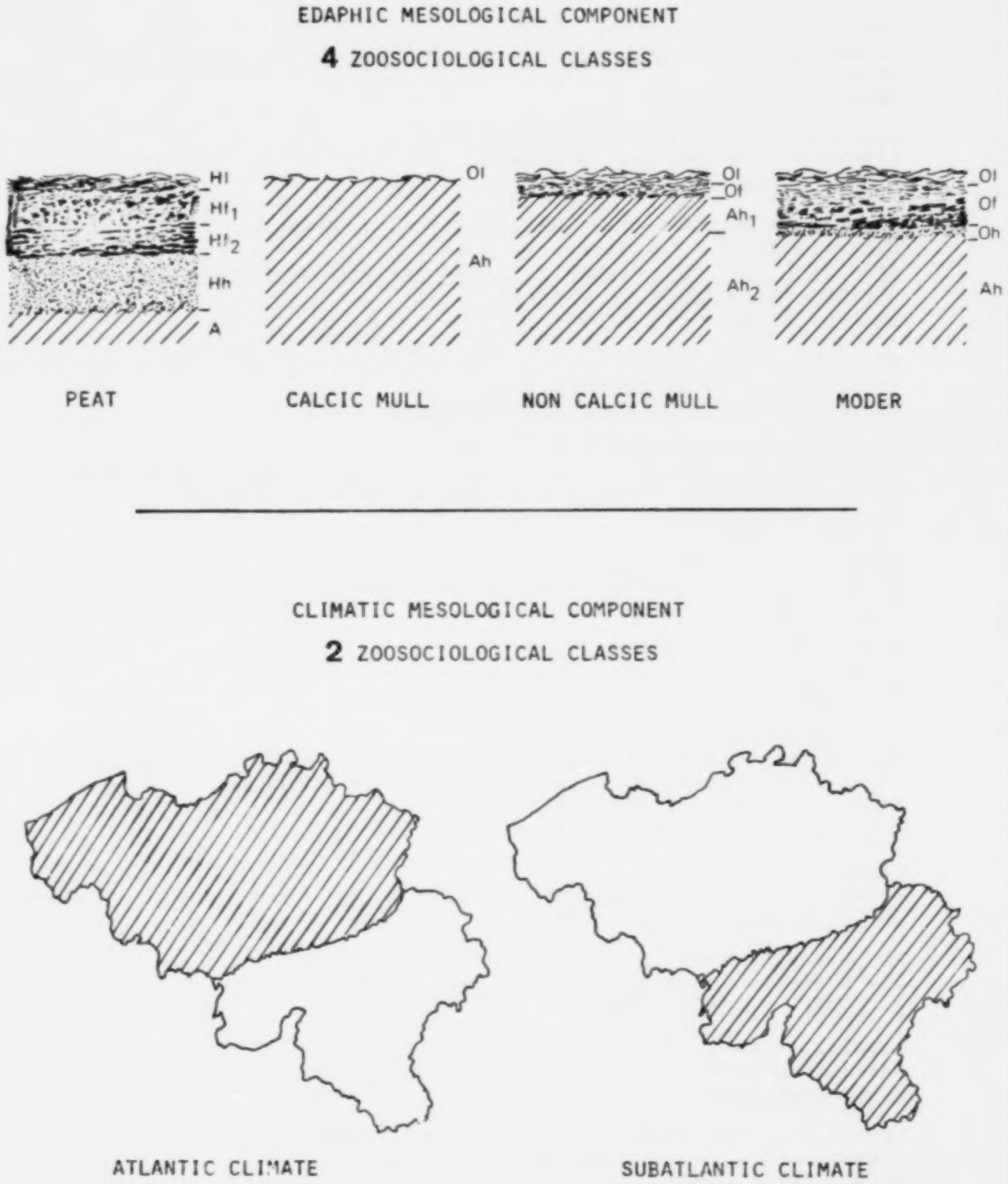

EDAPHIC MESOLOGICAL COMPONENT
4 ZOOSOCIOLOGICAL CLASSES
Hl
Hf1
Hf2
Hh
A
Ol
Ah
Ol
Of
Ah1
Ah2
Ol
Of
Oh
Ah
PEAT
CALCIC MULL
NON CALCIC MULL
MODER
CLIMATIC MESOLOGICAL COMPONENT
2 ZOOSOCIOLOGICAL CLASSES
ATLANTIC CLIMATE
SUBATLANTIC CLIMATE

Figure 4. - The zoosociological classes. Designation of the pedological horizons : Hl, dead peat mosses almost undamaged ; Hf, peat mosses which are less structured Hh, peaty matters ; Ah, mineral hemiorganic horizon ; Ol, almost undamaged leaves ; Of, more and more splitted up leaves ; Oh, very splitted up and humified substances.

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QUESTIONS and COMMENTS

M.B. BOUCHÉ: Quel est le pourcentage d'explication de chacun des quatre principaux axes de votre analyse factorielle?

G. WAUTHY: These percentages are respectively 15.50, 11.35, 8.11 and 7.37 for the first four axes of the reciprocal of the hemiedaphic releves. As Lebart et al. (1977) note these percentages permit an appreciation of the confidence associated with each ordination. In our case the percentages seem high enough for the first four axes. For the fifth and sixth axis the percentages (respectively 5.85 and 5.60) are lower and approximately the same.

POPULATION DYNAMIC AND METABOLIC CHARACTERIZATION OF COLLEMBOLA SPECIES IN A BEECH FOREST ECOSYSTEM

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INTRODUCTION

Soil ecological studies carried out within the framework of the International Biological Programme (IBP) mostly focused on population size and production biology of larger taxonomic units without much emphasis on the role of individual species. The increasing knowledge about the structure and function of natural ecosystems,however, has during the recent years stimulated the interest in species diversity and community structure. The soil and litter fauna is often extremely diverse, but attempts to explain the co-existence of the many species in terms of fundamental niches have been so disappointing that it has led to the formulation,"The enigma of soil animal species diversity" (Anderson 1975). The present paper does not pretend to solve this enigma but will emphasize the dissimilarities between some collembolan species living together in a Danish beech forest soil as regards various aspects of their population dynamics and production biology.

The results suggest that several of the ecological characters separating collembolan species are combined into sets of properties which relate to the depth distribution of the species. A classification of the collembolan fauna based on these ecological characters therefore parallels and mostly coincides with the classical morphological life-forms described by Gisin (1943).

The information of this paper is extracted from a comprehensive study of collembolan population ecology and energetics which will be published in more details elsewhere. The work was commenced as part of the "Hestehave beech forest ecosystem project" which is a major Danish contribution to the IBP.

The research site covers 1.5 ha of a pure c. 95 years old beech stand. The surface soil has the character of a typical mull. There is a sharp separation between the litter layer (L) and the mineral soil. F and H layers are not distinguishable, but the humus content of the mineral soil decreases gradually with depth. The forest floor is through the spring and the summer more or less completely covered by a field layer dominated by *Anemone nemorosa* L, *Melica uniflora* Retz,*Asperula* odorata L , and Carex silvatica Huds. More information about the site and the project may be found in Yeates (1972) and Thamdrup,Nielsen and Petersen (1975).

METHODS

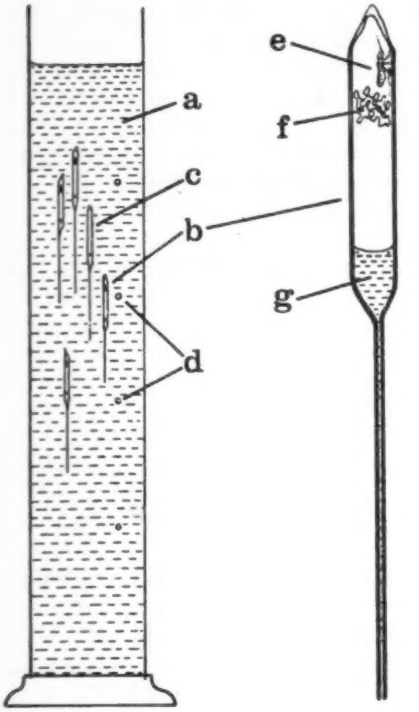
1. Field Population Estimation. 28 plots distributed in a stratified random pattern were sampled each month through a nearly biannual period. In each plot a litter sample (86.6 cm^2 surface area) and a core (10 cm^2 surface area) were sampled. The core was subdivided into L layer and two 3 cm thick layers of the mineral soil. A core to 15 cm depth was sampled seasonally. The sample units were extracted in high gradient extractors (Petersen 1978). Specimens mounted in slides were identified to species and as far as possible to sex and stage of reproductive development (Petersen,in press). The body lengths of the mounted specimens were measured by means of an ocular micrometer and converted to dry weight by the use of allometric regressions (Petersen 1975)

2. Culture Experiments. One to several eggs of some of the common species from the field site were transferred from stock cultures to small culture chambers kept at constant temperatures or at field temperatures (Petersen 1971,a). The size of specimens were measured regularly from eclosion to death by means of micro-photography (Petersen op.cit.). The cultures were mostly examined twice per week in order to check survival, and the production of exuviae and eggs. A yeast, Candida sp., extracted from the soil of the field site and cultured on agar plates, was in most cases used as food.

3. Respirometry. Measurements of oxygen consumption were carried out on single individuals by means of an open gradient diver method (Nexø, Hamburger and Zeuthen 1972) modified for terrestrial microarthropods (Petersen, in prep.). The method is based on the gradual sinking of a small ampulla containing the experimental animal in a linear density gradient made from a sodium-sulphate solution (FIGURE 1). The lower part of the ampulla contains 0.1 normal NaOH. The decreasing buoyancy of the ampulla caused by the respiration of the animal makes the ampulla sink at a rate proportional to the oxygen consumption. The movement of a control diver is used to correct for changes in temperature and atmospheric pressure. The changes in diver positions have been recorded by means of a time-lapse camera.

FIGURE 1. Open gradient diver respirometry.

a. Measuring cylinder with density gradient of Na_2SO_4 solution
b. Ampulla divers
c. Control diver
d. Density standards (glass beads)
e. Experimental animal
f. Porous material (polystyren)
g. 0.1 n NaOH



RESULTS

1. *Size and Composition of the Total Collembolan Population.* FIGURE 2 illustrates the density fluctuations of the total collembolan population through the biannual period (L + 0-6 cm mineral soil). It will be noted that the population reach maximum density during summer and autumn but was low during winter and early spring. A depression during late summer and early autumn of 1969 which coincided with a dry and hot period reduced the mean annual density of 1969 to about half of the mean density recorded in the following year. The total range of variation through the biannual period is $19. \times 10^3$ to $67. \times 10^3$ specimens per m^2. The biomass of the total collembolan population varied between 76 and 160 mg dwt. per m^2 in 1970.

   The composition of the collembolan fauna is listed in APPENDIX A. About 60 different species have been identified from the soil and litter within the rather homogeneous area of 1.5 ha. Several of these, however, have been found only occasionally. Others have been found regularly, but in low numbers. The two most abundant species *Tullbergia macrochaeta* (most common member of the *T.krausbaueri* species group; see footnote at APPENDIX A) and *I.minor* constitute together about 50% of the total number of *Collembola*. In terms of biomass, however, the dominance ranks are quite different with *T.flavescens* as the most dominant species followed by *L.lignorum.*

2. *Vertical Distribution.* FIGURE 3 shows the mean annual depth distribution of some of the most important species. In APPENDIX B the species have been classified into subjectively defined groups according to their depth distribution pattern. Juvenile specimens which generally constitute a major fraction of the average annual density have in all species a deeper distribution than adults. This has a special influence on the average annual depth distribution of the two sminthurid species *D.minuta* s.l. and *S. aureus* because adults of these species are more or less completely missing in the soil and litter during summer and early autumn. *D.minuta* seems to migrate from the forest floor to the tree canopy during early summer. The population of *S.aureus* may largely survive the summer as eggs.

   The two species which have the highest dominance values in terms of biomass, i.e. *L.lignorum* and *T. flavescens* are more or less confined to the litter layer (epedaphic). *T. macrochaeta* and *I. minor* which strongly dominate the collembolan fauna in terms of density clearly belong to the euedaphic group of species. The hemiedaphic category includes the majority of species occurring in the forest floor.

3. *Reproductive Periods*. FIGURE 4 and 5 exemplify two different patterns of seasonal changes in the size structure of col-

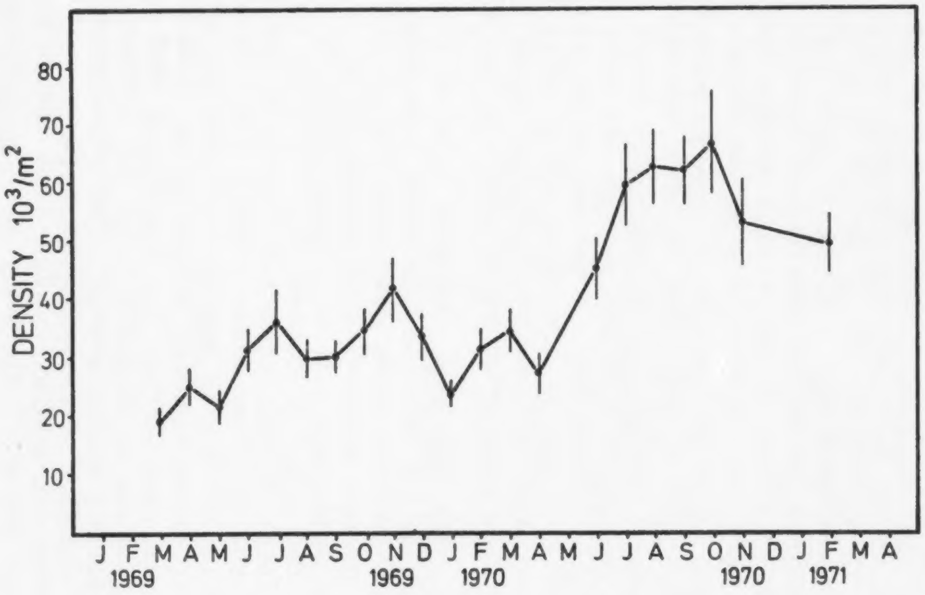
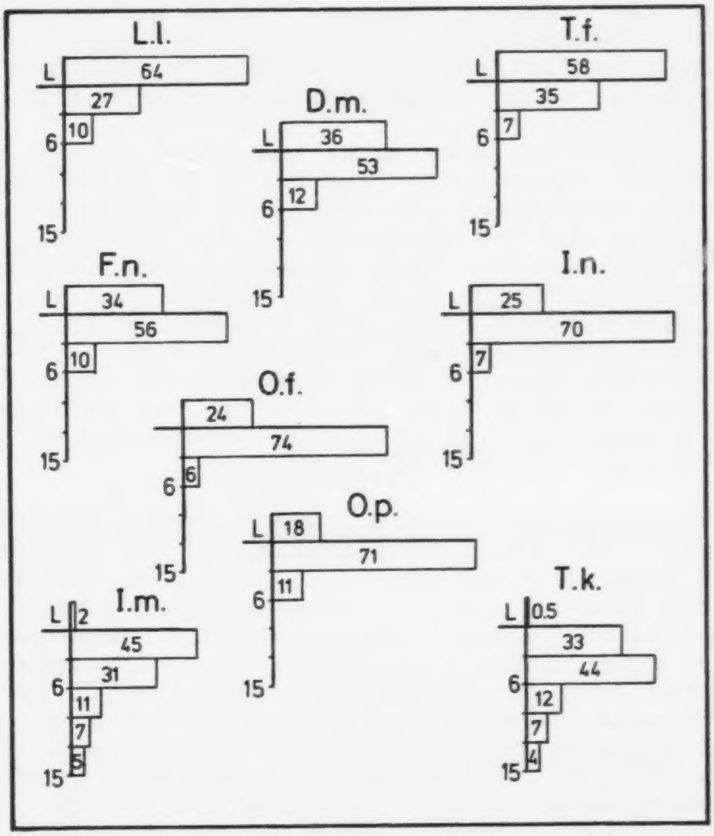


FIGURE 2. Density of the total collembolan population in the L layer and uppermost 6 cm of the mineral soil (March 1969 to February 1971). Arithmetic means ± standard errors.

FIGURE 3. Vertical distribution of selected species. Vertical axes indicate the litter layer (L) and 5 . 3 cm layers of the mineral soil. Horizontal bars illustrate the percentage contribution of each horizon to the total density of the species. L.l:*Lepidocyrtus lignorum*; T.f.:*Tomocerus flavescens*; D.m.: *Dicyrtomina minuta* s.l.; F.n.:*Folsomia nana*; I.n.: *Isotoma notabilis*; O.f.: *Onychiurus furcifer*; O.p.: *Onychiurus pseudovanderdrifti*; I.m.:*Isotomiella minor*; Tk: *Tullbergia krausbaueri* s.l.

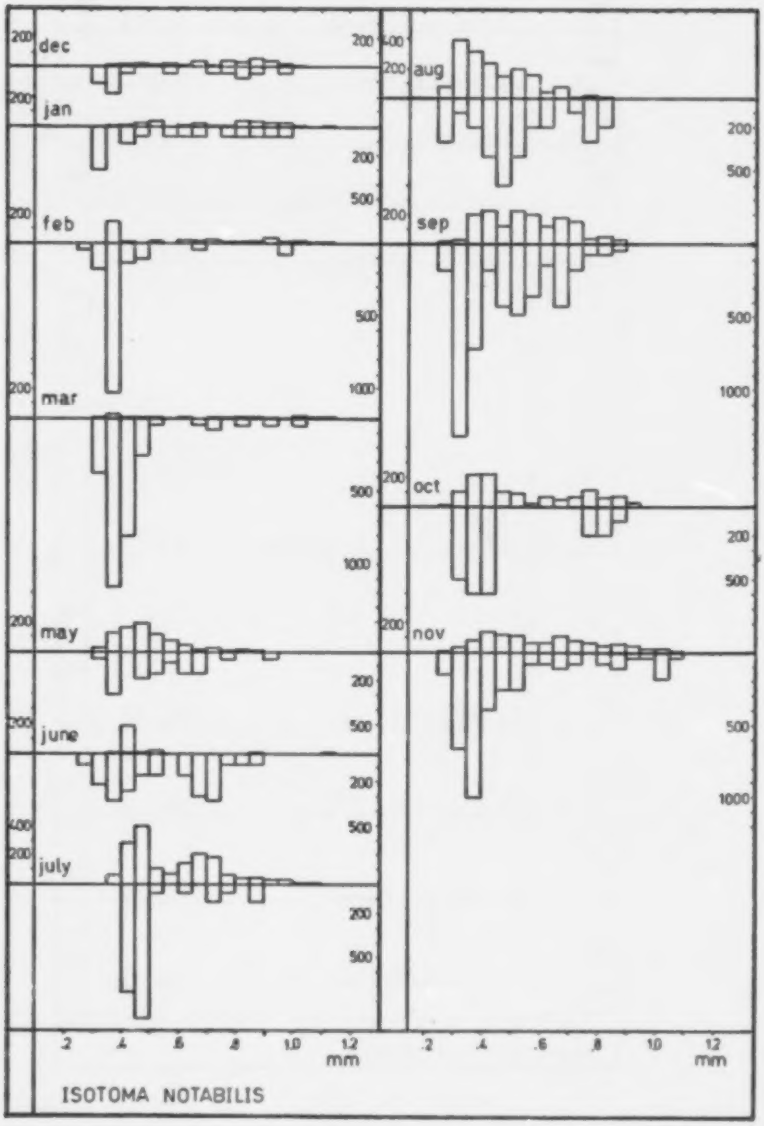


lembolan populations which reflect the occurrence of reproduction through the year. The *I.notabilis* population (FIGURE 4) includes throughout the year members of the smallest juvenile size classes. Thus, the reproductive period appears to cover most of the year. A similar pattern is shared by *I.minor* and *T. krausbaueri* s.l., i.e. the two most important euedaphic species. The epedaphic species *T. flavescens* (FIGURE 5) on the other hand has a more confined reproductive period. Most juveniles hatch in June and July, whereas the recruitment to the population in August, September,and October is less significant. Similar restricted reproductive periods are characteristic for the sminthurids *D. minuta* s.l. and *S. aureus* which mainly reproduce during late winter or very early in the spring. *O. furcifer* and *W. anophthalma* which are classified among the hemiedaphic species have also rather restricted recruitment periods culminating in June and August,respectively. The epedaphic *L. lignorum* has a more extended reproductive period from March to August. The hemiedaphic species *F.nana* seems to reproduce regularly from May to November.

Although each species of the beech forest floor may have a special reproductive phenology it seems justified to suggest a relationship between the depth distribution of the species and the extension of the reproductive period. Thus, it may be typical that euedaphic species reproduce more or less continuously through most of the year whereas the epedaphic species being more exposed to environmental fluctuations typically have seasonally restricted reproductive periods. Species with intermediate depth distributions cover a range from seasonally well defined reproduction (*O.furcifer*,*W.anophthalma*) to continuous reproduction through the year (*I.notabilis*).

4. *Mode of Reproduction*. *Bisexual and Parthenogenetical Populations*. The sex identification of the specimens from the field samples which was mainly based on the development of the genital aperture unveiled that several of the most abundant collembolan species in the Hestehave soil existed as pure female populations thus suggesting a parthenogenetic mode of reproduction (Petersen,in press). Parthenogenesis was confirmed for two of the species *I.notabilis* and *T.krausbaueri* by means of culture experiments (Petersen 1971, b). The Hestehave beech wood populations of the following seven abundant species can safely be attributed obligatory parthenogenetic reproduction:*Willemia anophthalma*, *Tullbergia macrochaeta*,*T. sylvatica*, *T.callipygos*, *Isotomiella minor*, *Isotoma notabilis*,and *Megalothorax minimus* but at least 8 additional less abundant species should probably be included among them. Thus,parthenogenetic reproduction comprise about 72% of the mean annual number of *Collembola* in the beech forest soil.

FIGURE 4. Isotoma notabilis. Size structure of the population December 1969 to November 1970. Horizontal axes define body length classes in mm. Vertical axes show number of specimens per m^2 in the litter layer (upwards from the horizontal axes), and the 0-6 cm horizons of the mineral soil (downwards).



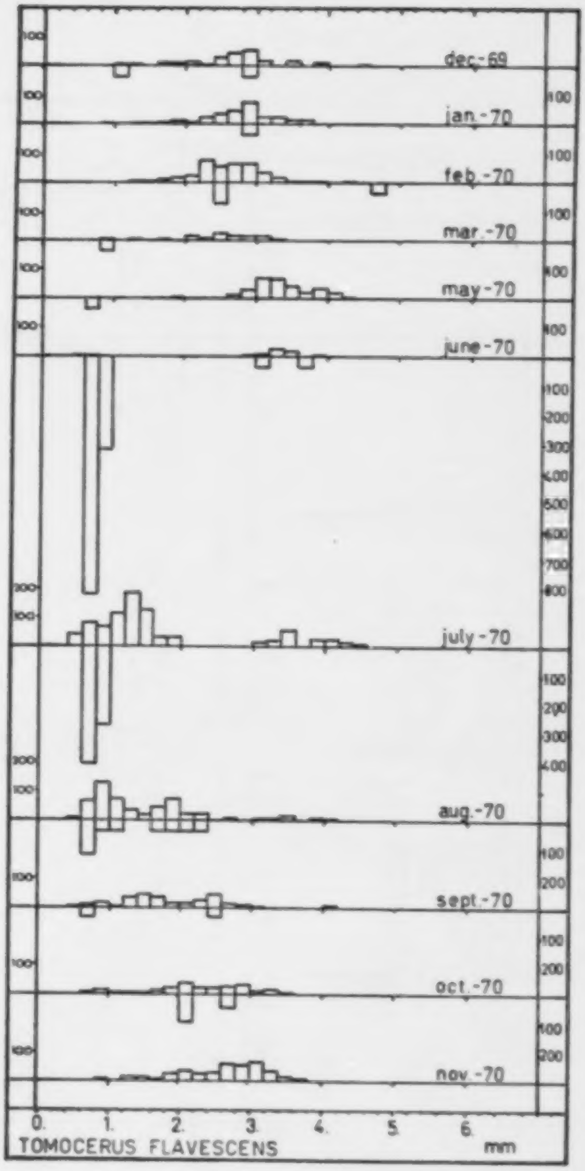


FIGURE 5. Tomocerus flavescens. Size structure of the population December 1969 to November 1970.For explanation see FIGURE 4.

female or male with "open" genital aperture and the smallest juvenile, or between females containing eggs and the smallest juvenile is considered. This sequence of species rather closely parallels the sequence of species ranked according to vertical distribution. Thus the epedaphic species are characterized by an extended development before maturity is reached, or if expressed inversely: the progeny of the epedaphic species is small compared with the smallest sexually mature adults. The euedaphic parthenogenetic species on the other hand produce progeny which is relatively large compared with the smallest egg producing females. The hemiedaphic species produce progeny of intermediate relative size.

The postmature growth which is illustrated by the ratios between the largest and the smallest females or males shows relatively small differences between species and seems not related to the depth distribution.

6. *Metabolic Rate*. Results from respiration measurements of some of the most significant collembolan species in the Hestehave beech forest floor (Petersen,in prep.)(FIGURE 9- 11) suggest that the metabolic rate is related to the depth distribution of the species. The relation between dry weight and oxygen consumption is described by the formula:

$$R = a \; . \; W^{b}$$

where R is oxygen consumption per individual per hour,
W is dry weight per individual
and a and b are constants.

The exponent b (pooled between temperatures) varies from 0.78 in *O.furcifer* to 0.96 in *T.flavescens*.

At all three temperatures and throughout the weight range *D. minuta* s.l. has the highest oxygen consumption followed by *L. lignorum*.The euedaphic *I.minuta* has at the three temperatures the lowest oxygen consumption of the measured species. The hemiedaphic species *I. notabilis*, *F. quadrioculata* s.l., and *O. furcifer* have intermediate respiratory rates. The metabolism of *T. flavescens* is more difficult to relate to the other epedaphic species,but the large adults have a high metabolic rate whereas the respiration of the small juveniles is relatively low.

Two characters obviously unite the parthenogenetic species: They are relatively small, and they live in the more protected strata of the forest floor. Only I.notabilis and especially W. anophthalma disagree with the euedaphic depth distribution by having a relatively large proportion of their populations in the litter layer. The populations of all epedaphic and most hemiedaphic species,however, include 30% to 50% males and seem restricted to a bisexual mode of reproduction.

5. Relative Size of Offspring. The size of newly hatched juveniles and sexually mature adults was estimated from examination of the mounted specimens from the field samples, and from measurements of specimens kept in culture (FIGURE 6 - 8).

Adults mounted on slides can be recognized by the development of the genital aperture (Petersen,in press). A distinction can often be made between "closed" and "open" genital apertures which indicates that the individuals were in a reproductively inactive or a reproductively active stage, respectively. In females possessing "open" genital apertures eggs may occasionally be recognized inside the mounted body. In males with "open" genital apertures an ejaculatory duct is usually distinct. The stages with "open" and "closed" genital apertures seem to alternate more or less regularly throughout the reproductive period of the animals (Mayer 1957, Snider 1973).

In the material of mounted specimens from the field samples the stage of reproductive maturity, however, is most safely defined by the smallest specimens with "open" genital apertures or with eggs visible within the ovaries. In the culture experiments reproductive maturity was defined by the first oviposition. The size of newly hatched individuals was measured within the first four days after eclosion.

FIGURE 6 - 8 illustrate the frequency of occurrence of the different developmental stages in three typical species. I. notabilis (FIGURE 7) exemplifies a type of development characterized by the occurrence of maturity in specimens which are only little larger than the newly hatched juveniles. T. flavescens (FIGURE 8) exemplifies the other extreme in which maturity is not reached until a considerable growth has occurred. O.furcifer (FIGURE 6) exemplifies an intermediate type.

APPENDIX C presents the weights of characteristic stages during the development from newly hatched juveniles to the largest adult specimens of some of the most important species in the Hestehave forest floor.In APPENDIX D the ratio between some of these values have been ranked according to the ratio between the smallest female (A) or male (B) and the smallest juvenile. The species maintain principally the same rank if the ratio between the smallest

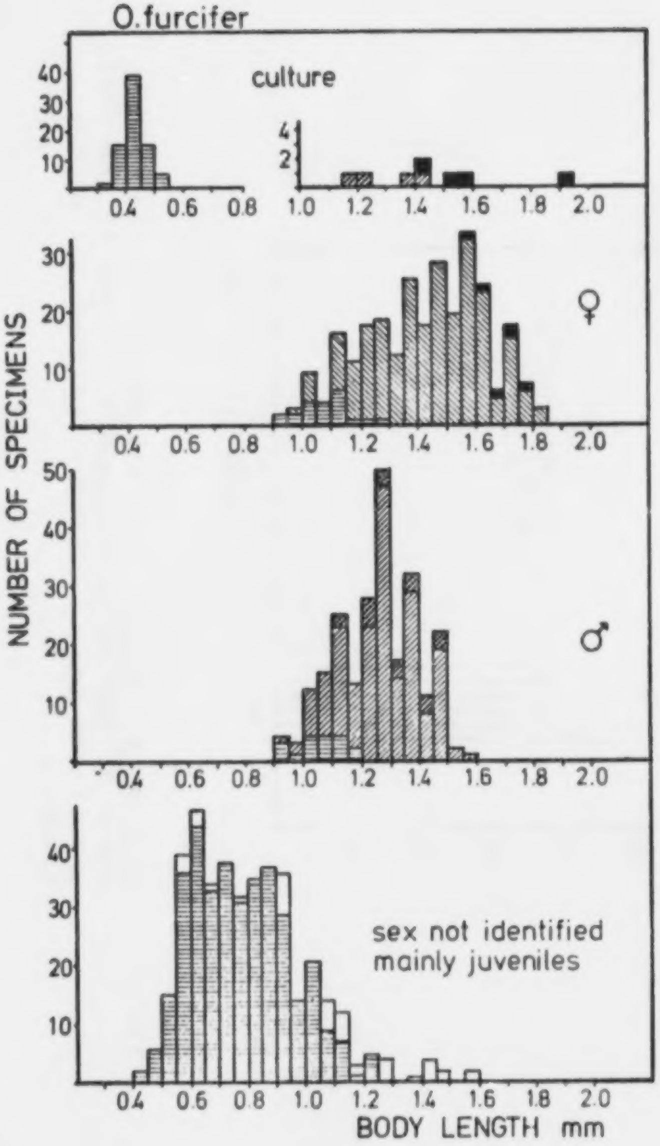


FIGURE 6.

Onychiurus furcifer. Size structure and the occurrence of various developmental stages in the field population and in cultures. The frequency distribution of the field population is based on the cumulated results from 11 samples (December 1969 to November 1970).

- ▤ juveniles. In the diagram representing culture experiments: Juveniles 0-4 days old
- ☐ sex or stage not identified
- ▨ males "closed" genital apertures see text
- ▩ males "open" genital apertures. For cultures: males coupled with females producing their first egg batch.

- ▨ females "closed" genital apertures
- ▩ females "open" genital apertures
- ■ females containing (producing) eggs. For cultures: females few days after first oviposition.

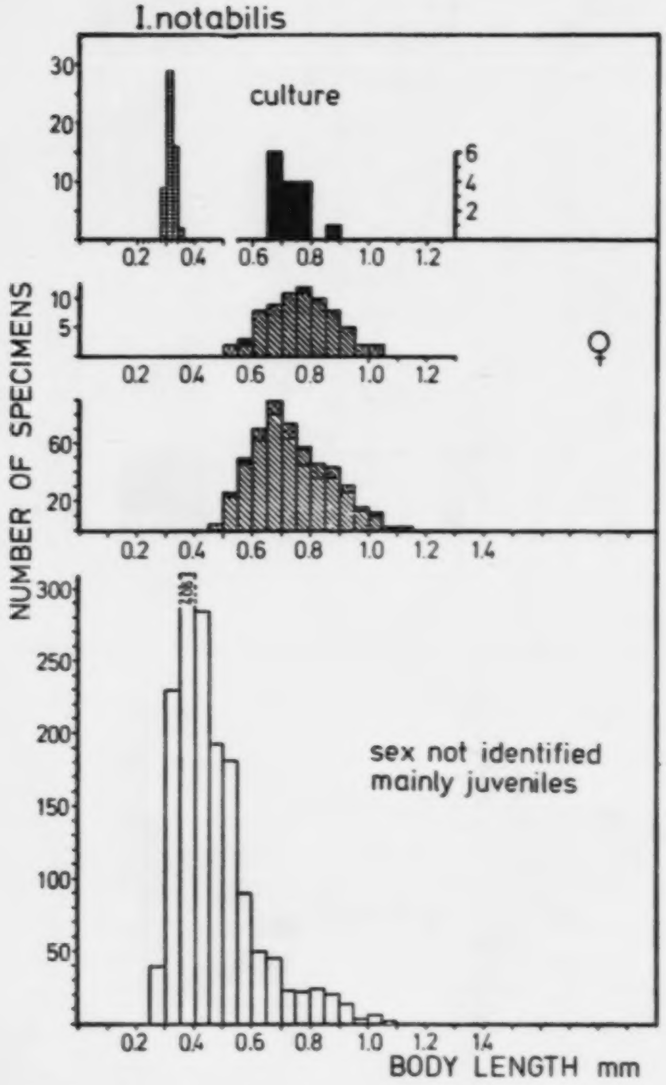


FIGURE 7. Isotoma notabilis. Size structure and the occurrence of various developmental stages in the field population and in cultures.For explanation see FIGURE 6.

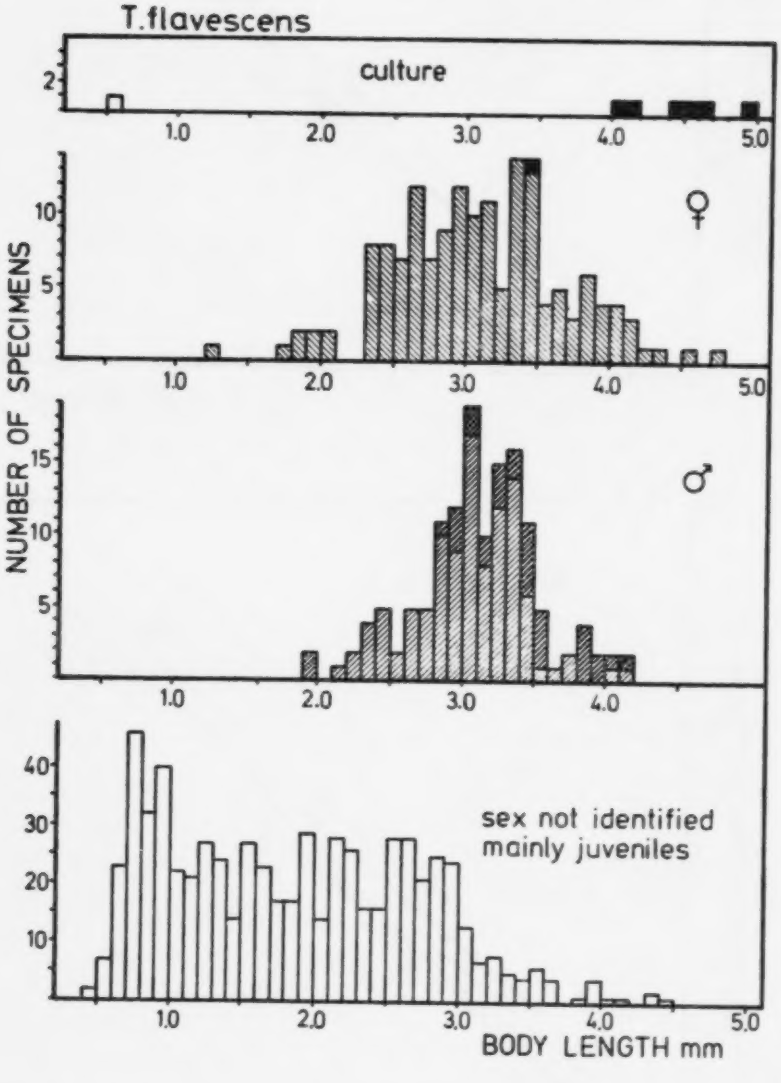


FIGURE 8. Tomocerus flavescens. Size structure and the occurrence of various developmental stages in the field population and in cultures. For explanation see FIGURE 6.

FIGURE 9. Relation between dry weight and oxygen consumption rate per individual in several collembolan species.

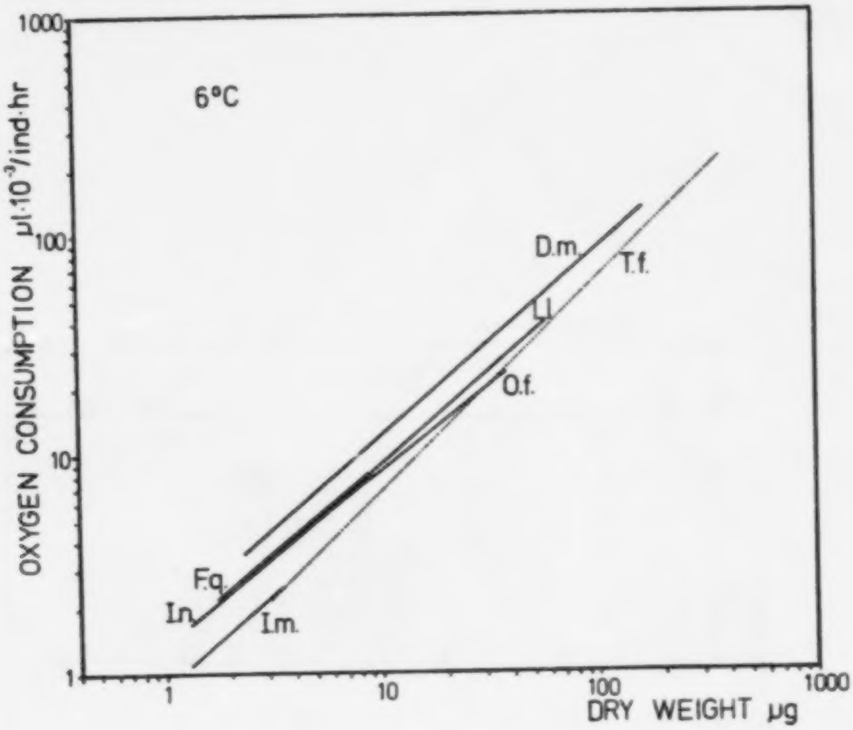
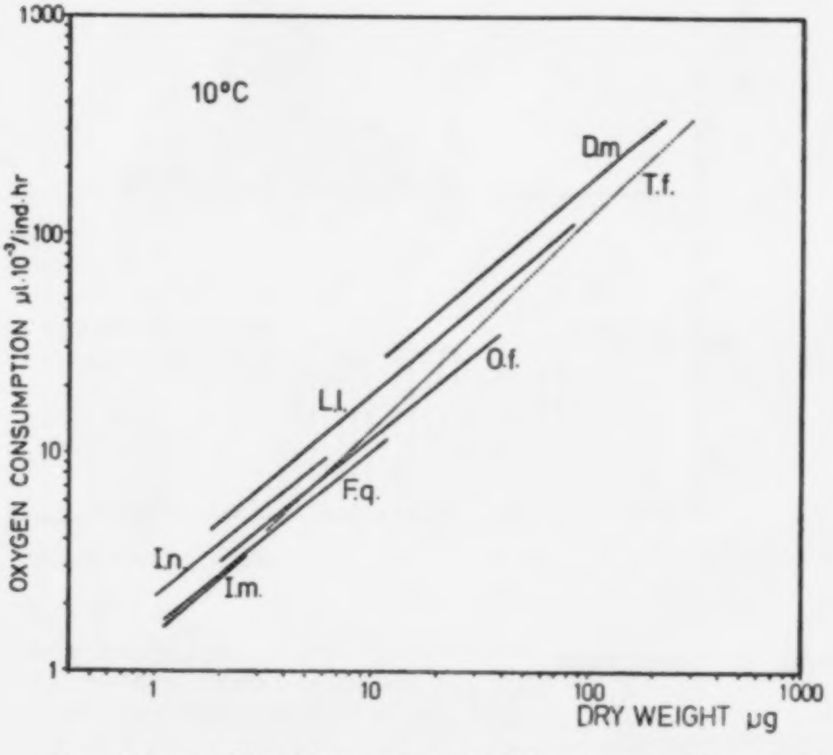


FIGURE 10.



For identification of abbreviations referring to species see FIGURE 3.

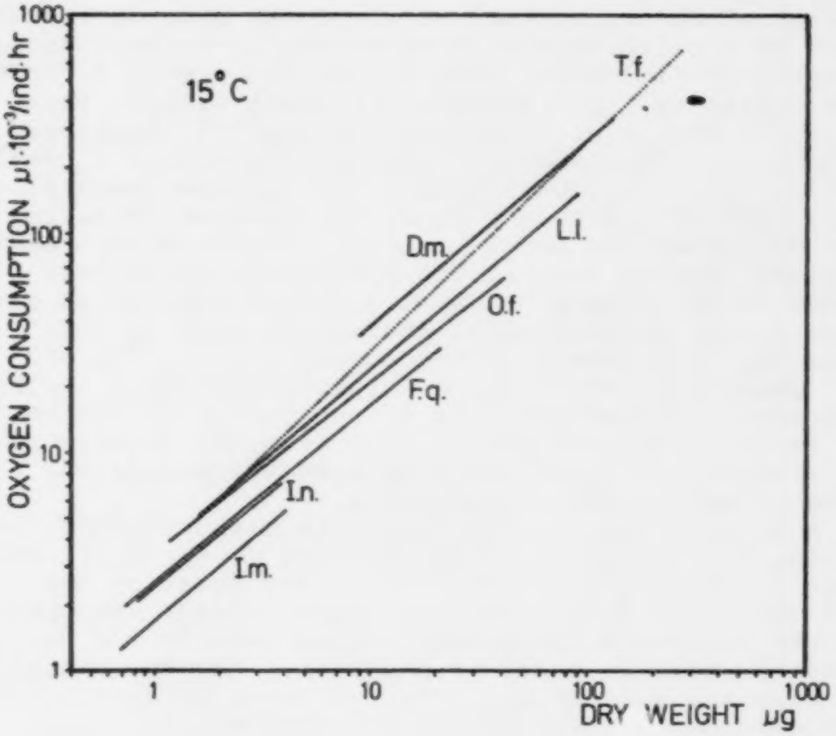


FIGURE 11. Relation between dry weight and oxygen consumption rate per individual in several collembolan species. 15°C.For identification of abbreviation referring to species see FIGURE 3.

DISCUSSION

The results presented above suggest that various aspects of collembolan population dynamics and energetics are interrelated and characterize groups of species with a common depth distribution. The relationship between these ecological characters and the depth distribution is paralleled by a relationship between sets of morphological and sensory physiological adaptations which were described and classified as "Lebensformen" by Gisin (1943). Thus, according to this classification the typical "Euedaphon" differ from the "Hemiedaphon" and the "Atmobios" by small size, reduction of limbs,antennae and furcula, lack of pigment, lack of scales and other specialized setae,reduction of ommatidiae and in return a strong development of chemical sensory organs. The ecological characters described in this paper may have a direct functional relationship with morphological characters such as body size and the development of locomotory organs. The ecological characters may also be mutually dependent so that one character automatically is a consequence of another. At the present state of insight, however, it is only possible to speculate about the causal relationships and adaptive values of these characters.

A govering ecological factor is without doubt the increasing environmental stability with depth. Dayly and seasonal fluctuations in temperature and moisture are leveled out. This will allow reproduction,egg development and growth through a large part of the year in the deeper soil layers where in contrast conditions for these activities near the surface are only favorable in restricted periods dependent on the actual climate, but in broad outline fixed by seasonal climatic changes.

Williams (1975) discussed the general occurrence of asexual and sexual reproduction in organisms and concluded that asexual reproduction is expected to be the optimal mode of reproduction in stable environments with mild natural selection whereas sexual reproduction is an adaptation to unpredictable environmental conditions and intense natural selection. The importance of parthenogenesis among the euedaphic species in the Hestehave forest might well be explained in the light of this hypothesis. However, another possible explanation is that the collembolan indirect spermatophore transfer mechanism is too inefficient to work among individuals of several species which probably live widely scattered in the complex system of soil interstices (Petersen,in press).

It is not yet possible to draw definite conclusions about the population dynamic consequences of the differences found between the size of progeny and the first reproductive adult stage. Preliminary data from cultures suggest that the small relative size of the first reproductive stage found in euedaphic species does not mean a very short generation time in comparison with the generation time of hemiedaphic species. Further, the first ovipositions of the euedaphic species T. macrochaeta and I. notabilis comprise very few eggs (mostly 1-2) compared with the number of eggs produced in the first oviposition by the hemiedaphic O. furcifer (13-18 eggs). The average number of eggs per oviposition during the whole life time appears also to be lower in T. macrochaeta and I. notabilis than reported for hemiedaphic and euedaphic species (Gregoire-Wibo 1977, Hale 1965).Although it is less well documented that the total average egg production per female is lower in euedaphic than in hemiedaphic and epedaphic species it seems fairly certain that the small size at which egg production begins in these small euedaphic species is not equal to a higher reproductive potential than found in hemiedaphic and epedaphic species.

The small individual size at the start of the reproductive period combined with a small number of eggs per oviposition may be an adaptation to the narrow space of the interstices. The low number of eggs per oviposition is compensated for by an extended period of reproduction with repeated ovipositions which is favoured by the constant environmental conditions in the deeper layers of the soil. The differences in metabolic rate between euedaphic,hemiedaphic and epedaphic species probably reflect the general level of activity of the species. Epedaphic species move a lot more about than euedaphic species in order to escape from predators or quickly changing environmental conditions or in search for food.

Collembolan species living superficially have according to Bödvarsson (1970) a higher percentage of fungal hyphae and spores in their guts than species living deeper in the soil. Fewer specimens of the surface forms than of the deeper living forms, however, have their guts filled with consumed material. These results have largely been confirmed by preliminary observations of the gut contents of the Collembola from the Hestehave beech wood.The observations may be interpreted in the following way based on Bödvarsson (op.cit.): The euedaphic species are obliged to feed more or less continuously on a poor food, whereas the epedaphic species as the other extreme must spend much time and energy in search for better quality foods. In this way the feeding biology may help to explain the different levels of metabolic avtivity.

CONCLUSIONS

The relationships between various ecological characters of Collembola which have been described and discussed above are summarized in the following somewhat idealized scematical list in which general properties of superficially living (epedaphic) Collembola are contrasted with the corresponding properties of the true interstitial soil species (euedaphic species). The hemiedaphic species will in general terms have intermediate characters.

	Epedaphic	Euedaphic
vertical distribution	surface, litter	soil interstices
size of specimens	large	small
reproduction	bisexual	parthenogenetical
	small progeny	large progeny
	many eggs(?)	few eggs(?)
	seasonally defined	throughout the year
metabolic activity	high	low
food	high quality	low quality
	dispersed	omnipresent

SUMMARY

The paper presents results extracted from a comprehensive study of collembolan ecology and energetics in a Danish beech wood.

The population density varies from $19 . 10^3$ to $67 . 10^3$ per m^2 through a biannual period. The biomass varies through one year from 76 to 160 mg dwt. per m^2. About 60 species were found within the research site of 1.5 ha.

The most abundant species are classified according to their vertical distribution patterns as epedaphic (surface and litter species) hemiedaphic (populations concentrated around the soil-litter interface), and euedaphic (populations concentrated in the mineral soil interstices).

The variations in size structure of different species populations show that epedaphic and some hemiedaphic species have seasonally well defined reproductive periods whereas other

hemiedaphic and the euedaphic species reproduce through most of the year. Parthenogenetical reproduction is typical for euedaphic species in contrast to most hemiedaphic and epedaphic species which reproduce bisexually. The small euedaphic species produce large progeny which only weighs four to six times less than the smallest reproductive adults. Epedaphic species in contrast produce relatively small juveniles which need to increase many times in weight before maturity is reached. Hemiedaphic species produce progeny of intermediate size.

Results from respirometry experiments carried out by means of an open gradient diver method suggest that the rate of oxygen uptake decrease from epedaphic through hemiedaphic to euedaphic species of Collembola.

The increase of environmental stability with depth is considered a governing factor responsible for the differences found between collembolan species attached to different horizons of the soil. Further, the influence of the narrow space in the soil interstices is included as a significant factor. The mode of reproduction and type of development from juvenile to reproductive adult are discussed in the light of these environmental properties.

The high metabolic rate of the epedaphic species seems to have relation to the general locomotory activity of the species including the feeding biology which involves search for dispersed high quality food items.

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APPENDIX A

Density dominance rank of collembolan species found in the Hestehave research site December 1969 to November 1970. Litter and uppermost 6 cm of the mineral soil. The taxonomy is mainly based on Gisin (1960).

		dominance %
1.	*Tullbergia krausbaueri* (Börner)$^{+}$s.l.	37.1
2.	*Isotomiella minor* (Schäffer 1896)	21.5
3.	*Isotoma notabilis* Schäffer 1896	6.9
4.	*Folsomia nana* Gisin 1957	5.3
5.	*Megalothorax minimus* Willem 1900	4.2
6.	*Lepidocyrtus lignorum* (Fabricius 1775),Gisin 1964	3.1
7.	*Sminthurinus aureus* (Lubbock 1862)	2.6
8.	*Onychiurus furcifer* (Börner 1901)	2.5
9.	*Pseudosinella alba* (Packard 1873)	2.4
10.	*Willemia anophthalma* Börner 1901,Hüther 1962	1.9
11.	*Tullbergia callipygos* Börner 1902	1.6
12.	*Dicyrtoma minuta* (O.Fabricius 1783)$^{++}$s.l.	1.5
13.	*Onychiurus pannonicus* Haybach 1960	1.3
14.	*Tomocerus flavescens* (Tullberg 1871)	1.3
15.	*Onychiurus armatus* (Tullberg) Gisin 1952	1.1
16.	*Folsomia quadrioculata* (Tullberg 1871),Gisin 1957	1.0
17.	*Onychiurus pseudovanderdrifti* Gisin 1957	1.0
18.	*Friesea mirabilis* (Tullberg 1871)	0.5
19.	*Onychiurus absoloni* (Börner 1901)	0.5
20.	*Isotoma* sp. (*olivacea* group)	0.5
21.	*Anurida pygmaea* (Börner 1901)	0.4
22.	*Xenylla grisea* Axelson 1900	0.2
23.	*X. boerneri* Axelson 1905	0.2
24.	*Tullbergia denisi* (Bagnall 1935)	0.2
25.	*Folsomia candida* Willem,Lawrence 1973	0.2
26.	*Folsomia monosetosa* Rusek 1966	0.2
27.	*Neanura muscorum* (Templeton 1835)	0.1
28.	*Willemia aspinata* Stach 1949, Hüther 1949	0.1
29.	*Orchesella flavescens* (Bourlet 1839)	< 0.1
30.	*Neelus minutus* Folsom 1901	< 0.1
31.	*Willemia intermedia* Mills 1934,Hüther 1962	"
32.	*Onychiurus serratotuberculatus* Stach 1933	"
33.	*Isotoma sensibilis* (Tullberg 1876)	"
34.	*Dicyrtoma fusca* (Lucas 1842)	"
35.	*Proisotoma minima* (Absolon 1901)	"
36.	*Sminthurinus flammeolus* Gisin 1957	"
37.	*Tomocerus longicornis* (Müller 1776)	"
38.	*Hypogastrura purpurescens* (Lubbock 1867)	"
39.	*Pseudachorutes dubius* Krausbauer 1898	"
40.	*Folsomia* cf. *spinosa* Kseneman 1936	"

Accidental species.(Not ranked after dominance).

Hypogastrura cf. *denticulata* (Bagnall 1941)
Friesea claviseta Axelson 1900
Tullbergia (*Wankeliella*) *peterseni* Rusek 1975

Isotoma cf. *cinerea* (Nicolet 1841)
Isotoma viridis Bourlet 1839
Isotomurus palustris (Müller 1776)
Entomobrya corticalis (Nicolet 1841)
Orchesella cincta (Linné 1758)
Willowsia migromaculata+++ (Lubbock 1873)
Seira domestica+++ (Nicolet 1841)
Heteromurus nitidus (Templeton 1835)
Lepidocyrtus lanuginosus (Gmelin 1788),Gisin 1964
Lepidocyrtus violaceus Lubbock 1873,Gisin 1964
Pseudosinella petterseni Börner 1901
Sminthurides pumilis (Krausbauer 1898)
Sminthurides malmgreni (Tullberg 1876)
Arrhopalites caecus (Tullberg 1871)
Bourletiella bicincta (Koch 1840)
Entomobrya multifasciata (Tullberg 1871)

+ *Tullbergia krausbaueri* s.l.: According to Rusek (1971, 1974,1976) this taxon is a composite group of species. The Hestehave material is mainly composed of *T.macrochaeta* (Rusek 1976) but includes also T.*krausbaueri* (Börner) *sensu* Rusek 1971 and *T. sylvatica* Rusek 1971.

++ *Dicyrtomina minuta* s.l.: The material mainly agree with *D. saundersi* (Lubbock 1862) but include a number of specimens identified as *D. minuta* (O. Fabricius 1783) and *D. ornata* (Nicolet 1841). The identity of these taxa as separate species is questionable.

+++ The appearence of these synanthropic species in the extracted samples may be due to accidental immigration from the laboratory during extraction.

APPENDIX B

Important collembolan species ranked according to vertical distribution. Percent annual mean density in litter (L) and the two uppermost three cm layers of the mineral soil. (Definition of terms: epedaphic: Distribution concentrated in or at the surface of the L layer; hyperedaphic: Main distribution on plants above the soil and litter; hemiedaphic: Main distribution around the soil-litter interface; euedaphic: Main distribution in the mineral soil).

		L	0-3 cm	3-6 cm
epedaphic	L.lignorum	64	27	9
	T. flavescens	58	35	7
juv.:hemidaphic ad.:epedaphic to hyperedaphic	D.minuta s.l.	36	51	12
	S. aureus	27	56	17
hemiedaphic	W. anophthalma	44	51	5
	F.quadrioculata	40	58	2
	F. nana	34	56	10
	I. notabilis	25	68	7
	O. furcifer	24	71	6
	O.pseudovanderdrifti	18	71	11
	P. alba	14	66	20
euedaphic	M. minimus	5	66	29
	I. minor	2	58	40
	O.armatus s.str.	3	52	45
	T. callipygos	3	44	53
	T.krausbaueri s.l.	< 1	42	57
	O.pannonicus	< 1	30	70

APPENDIX C

Dry weights (µg) of characteristic developmental stages in the collembolan life cycle. Weights calculated from body length data according to Petersen 1975. Data from analyses of field populations.
Suffix c: genital orifice closed. Suffix o: genital orifice open
Suffix e: eggs visible inside body of cleared specimens.

	min.juv.	min.♀ c.	min.♀ o	min.♀ e	max. ♀ (=max. specimen)	min.♂ c	min.♂ o	max. ♂
O. furcifer	0.59	4.85	-	16.0+++	34.7	4.85	8.24	21.9
O.pseudovanderdrifti	0.76	5.27	-	14.4	50.5	4.65	10.7	30.0
T.krausbaueri s.l.+	0.058	0.11	0.27	0.31	1.50	-	-	-
T.callipygos	0.42	2.51	2.51	-	21.9	-	-	-
F.nana	0.09	0.70	1.29	3.11	8.46	0.87	0.87	4.14
F.quadrioculata	0.15	1.06	3.11	6.05	14.95	1.29	1.90	7.60
I.minor	0.10	0.44	0.58	1.18	3.63	-	-	-
I. notabilis	0.22	0.70	0.87	1.06	8.02	-	-	-
L.lignorum	0.21	4.00	-	9.35	82.7	4.00	4.00	54.2
T.flavescens	0.66	27.4	-	176.	424.	36.8	104.	293.
D. minuta s.l.++	1.11	15.5	-	-	317.	15.5	18.0	199.

+ ++ see appendix A.

+++ min. ♀ e from culture experiment; min. ♀ e from field data: 21,9.

APPENDIX D

Ratios between dry body weights of characteristic developmental stages in the collembolan life cycle. Data from analysis of field populations. (For explanation see APPENDIX A)

A: Female ratios, ranked according to $\frac{\text{min.♀ c}}{\text{min.juv.}}$ ratio.

	$\frac{\text{min.♀ c}}{\text{min.juv.}}$	$\frac{\text{min.♀ o}}{\text{min.juv.}}$	$\frac{\text{min.♀ e}}{\text{min.juv.}}$	$\frac{\text{max.♀}}{\text{min.juv.}}$	$\frac{\text{max.♀}}{\text{min.♀}}$	$\frac{\text{max.♀}}{\text{min.♀ e}}$
T.flavescens	42.	-	267.	642.	16.	2.4
L.lignorum	19.	-	45.	394.	21.	8.8
D.minuta s.l. ++	14.	-	-	286.	21.	-
O.furcifer	8.2	-	27.+++	59.	7.1	2.2
F.nana	7.8	14.	35.	94.	12.	2.7
F.quadrioculata	7.1	21.	40.	100.	14.	2.5
O.pseudovanderdrifti	6.9	-	19.	67.	9.6	3.5
T.callipygos	6.0	6.0	-	52.	8.7	-
I.minor	4.4	5.8	12.	36.	8.	3.1
I.notabilis	3.2	4.0	4.8	37.	12.	7.6
T.krausbaueri s.l.+	1.9	4.7	5.3	26.	14.	4.8

+ ++ see appendix A. +++ min. ♀ e from culture experiment.

APPENDIX D cont.

B: Male ratios ranked according to $\frac{\text{min.♂ c}}{\text{min.juv.}}$ ratio.

	$\frac{\text{min.♂ c}}{\text{min.juv.}}$	$\frac{\text{min.♂ o}}{\text{min.juv.}}$	$\frac{\text{max.♂ o}}{\text{min.juv.}}$	$\frac{\text{max.♂}}{\text{min.♂ o}}$
T.flavescens	82.	158.	444.	2.8
L.lignorum	19.	19.	258.	14.
D.minuta s.l.	14.	16.	179.	11.
O.pseudovanderdrifti	9.7	14.	40.	2.8
F.nana	9.7	9.7	46.	4.8
F.quadrioculata	8.6	13.	51.	4.0
O.furcifer	8.2	14.	37.	2.7

ACTIVITY OF SOIL BIOTA DURING SUCCESSION FROM OLD FIELD TO WOODLAND

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INTRODUCTION

The purpose of this study, carried out in 1966 and 1967 at Molslaboratoriet, Jutland, Denmark, was two-fold. Firstly as a contribution towards a survey of the ecological conditions in the estate which surrounds the Mols laboratory and secondly, in the context of the International Biological Programme, to test the usefulness of "soil respiration" (carbon dioxide emission from the soil) as a general index of decomposition activity in the soil. Since the work was done much has been published on the latter topic but very little of it concerns relations between soil respiration and succession, especially those features which follow changes in agricultural practice. Also there are problems and assumptions about the interpretation of soil respiration methods which remain controversial and for which additional data may be helpful. In what follows I shall discuss briefly the features of the study area and the implications of the survey results and then some details of the technique used and its strengths and weaknesses in the context of preliminary surveys.

THE STUDY AREA

The Mols Laboratory estate of some 150h.a. is fully described by Thamdrup (1947). From the point of view of this study the main features are that it is largely covered by an acid sandy soil much of which has been cultivated in the past but has been allowed to revert to heath and woodland. At the time of the study almost half the area was being maintained as meadows for grazing or haymaking, dominated by *Agrostis tenuis*, *Alepocurus pratensis*, *Festuca elatior* and *Holcus lanatus* with some other grasses in local areas. The remaining sites were chosen in the region of Simmons Havsti and showed stages of a succession (following abandonment of cultivation) through bare sand, *Corynephrus canescens* and lichens(2) to *Calluna vulgaris*(6) followed by invasion by shrubs, including *Sarothamnus* (= *Cytisus*) *scoparius*(7) (believed to be a more vigorous variety from Southern Europe) and *Juniperus communis*(8) and by trees, especially *Pinus sylvestris*(9) and *Quercus petraea*(10).

Two sets of sampling areas were chosen to represent the meadows and the *Calluna* series and are numbered 1 - 5 and 6 - 10 respectively in this paper. With the help of maps and air photographs loaned by Professor Thamdrup and the recollections of Her Clausen Koch and Her Lauersen the dates of last cultivation of four meadows were established.

In the tables which follow data are given in the order:-

1. Krumehalden (3 years since cultivation).
2. Kjællinge-Agre (nearly pure *Corynephrus*).
3. Langbakke (6 years).
4. Kallebodder (5 years).
5. Horsehuller (over 6 years).

(For details see Thamdrup 1947).

Of these areas, Kjællinge-Agre was vegetated with *Corynephrus canescens* and thus represented the first stage of the succession through *Calluna* to woodland. In each meadow three widely spaced localities were selected and a transect line established, along which three sets of three adjacent bimonthly samples were taken randomly. Thus 45 samples were taken on five occasions; total 225. In addition, the October/November samples were used to test the value of allowing a "settling period" before taking readings (see below).

In the case of the *Calluna* succession series, samples were taken on four occasions in addition to the extra series used to test the disturbance effect.

The measuring technique

The method used for measuring"soil respiration" was briefly described in Brown & Macfadyen (1969) and is basically that of Anderson (1973), whose paper includes a useful survey of the history and characteristics of the method. Basically it derives from Haber's (1958)and Witkamp's (1966a, b) techniques and from Conway's micro-diffusion method (1950) and consists of insertion of small open-ended plastic cylinders ($25cm^2$ area by 10cm height) into the soil where they normally remain for a period of months. When a reading is to be taken an airtight cap is fitted from which a small glass dish is suspended. Usually 5ml. of approximately N/10 Potassium hydroxide solution containing excess Barium chloride and phenolphthalein/thymolphthalein indicator is supplied to the dish through a small hole, otherwise covered by a greased glass plate. After a measured period of one or two hours the alkali is back titrated rapidly in the field with Hydrochloric acid using a light portable microburette designed for the purpose. The amount of carbon dioxide is calculated from the reduction in strength of the alkali after allowing for the results of blank determinations.

On each occasion temperatures are taken at the beginning and end of the absorption period by thermistor thermometer between each triplet of samples at the soil litter interface and respiration data are calculated both with and without a "temperature correction" to $10^{\circ}C$. In other words the corrected readings are multiplied by a factor which assumes a Q_{10} of 2, the factor being 2 at $0^{\circ}C$, 1 at $10^{\circ}C$ and 0.5 at $20^{\circ}C$ and proportionately at intermediate temperatures according to the formula

$$\log_{10} Q_{10} = 2 = 10(\log Y_1 - \log Y_2) \frac{1}{x_1 - x_2}$$

in which Y_2 is the standard unit rate at $x_2 = 10^{\circ}C$ and Y_1 is the intermediate temperature.

The consistency of the "corrected temperatures" over the annual cycle provides a direct indication of the extent to which "spot" readings might prove of wider application as an index of respiration for a particular site. The choice of $Q_{10} = 2$ is justified by experiments both in the laboratory and the field and is usually accepted by other authors (e.g. Anderson 1973)and Reiners (1968) but see Witkamp (1966b) for contrary results and Mindermian & Vulto (1973). Shade from direct sunlight is provided by aluminium foil if necessary. All readings were started between 1100 and 1300 hrs. This procedure adequately deals with the needs of the local survey, but in the broader context of testing the method for wider use in unknown habitats it is also desirable to know whether readings taken immediately after insertion of the cylinders bear a consistent relationship to those after long exposure because this might permit a surveyor to complete readings in a single visit and operate with far fewer cylinders. Therefore, in addition to the readings made as above, additional ones were made in October and November by inserting fresh cylinders into undisturbed soil and immediately commencing the absorption procedure. The rationale behind this was simply that previous experiments had shown a rise in "respiration" over about six days followed by a fall to about one-third of the peak level by the end of two weeks. Also it is well-known that a burst of microbial activity follows disturbance of soil in laboratory respirometer experiments. In fact, as shown below, there proved to be a rather consistent relationship between the "disturbed" and the "undisturbed" readings on the same dates.

Special treatment was required in the case of the Pinus site because the very deep and long-leaved litter under these trees was impossible to manage in the normal respirometer tubes. Readings in these areas were therefore taken by removing the litter from an area of $100cm^2$ and measuring its carbon dioxide emission separately in a glass dish covered with a sheet of glass. The normal cylinders were then inserted into the F & H layers and soil below the litter and treated in the usual way. Results were expressed both as the separate component contributions and as the total of the two; correcting for the larger area of litter and for the disturbance effect.

RESULTS

The "soil respiration" data for the ten vegetation types (numbered in the order of the five meadows followed by the succession series through Calluna to Oak (= 10)) are summarised in Table 1 and Figure 1. These figures all refer to cores which were "undisturbed", that is were allowed to settle and measurements made by carefully placing lids on the tubes without moving these in the soil.

TABLE 1.

Bi-monthly soil respiration data from the ten vegetation types. Each figure is the mean of nine readings (three adjacent cores at three distinct sites) on each occasion. On each occasion the crude data are ml $CO_2/25cm^2/hr$ and the corrected figures are adjusted by a $Q_{10} = 2$ function to 10°C. The Columns 9a and 9b refer to soil and litter under pine respectively (see text). Temperatures °C in brackets are means of nine readings.

	Grassland Sites					"Succession" series					
Site No.	1	2	3	4	5	6	7	8	9a	9b	10
Oct.	(4.3°)	(3.9°)	(4.0°)	(4.1°)	(4.0°)	(4.9°)	(5.5°)	(7.3°)	(6.4°)		(6.5°)
Crude	159	102	145	166	146	145	173	249	186	375	251
Corrected	237	155	219	250	221	205	244	313	231	203	320
Jan.	(-0.2°)	(-0.2°)	(-0.2°)	(-0.2°)	(-0.2°)	(1.4°)	(1.6°)	(2.2°)	(1.9°)		(2.2°)
Crude	116	102	112	130	104	113	150	192	144	313	147
Corrected	236	207	226	271	210	204	268	330	252	169	252
April	(6.6°)	(11.6°)	(7.3°)	(7.3°)	(7.8°)	(6.2°)	(5.9°)	(5.8°)	(5.4°)		(6.7°)
Crude	304	419	357	358	365	181	234	226	212	119	278
Corrected	401	390	420	434	419	236	311	301	291	64	350
June	(20.2°)	(26.1°)	(21.5°)	(21.4°)	(21.3°)	(21.3°)	(21.3°)	(21.0°)	(19.7°)		(20.6°)
Crude	327	229	248	407	336	424	616	627	584	269	671
Corrected	155	65	109	192	144	194	280	293	296	145	321
August	(16.2°)	(22.0°)	(18.3°)	(19.2°)	(16.3°)						
Crude	813	632	772	1029	1041						
Corrected	501	286	437	539	618						

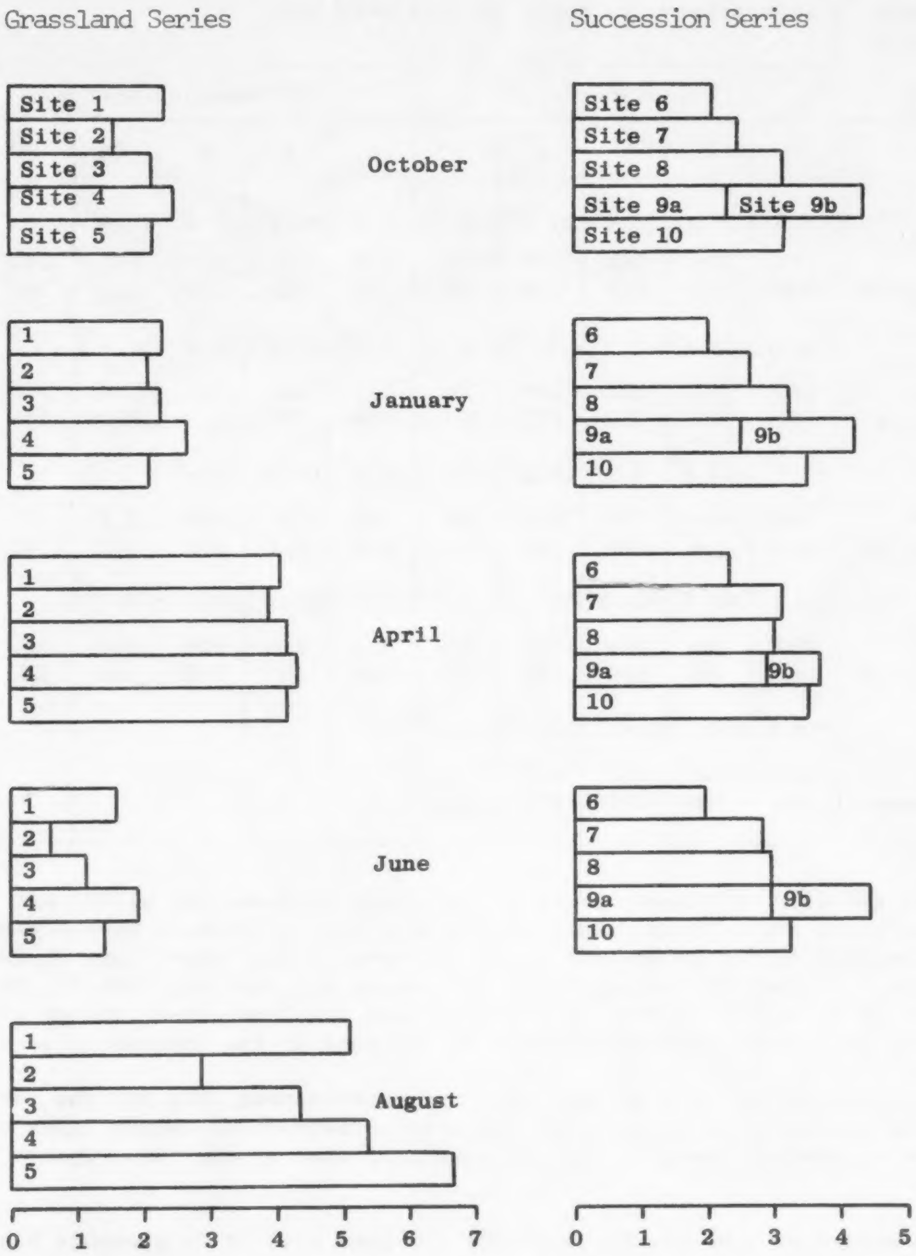
The two sets of figures refer to the crude estimate (of ml CO_2 per $25cm^2$ sample per hour) and to temperature corrected estimates derived by applying the Q_{10} function to the crude data using the mean of the temperature at the soil-litter interface at the beginning and end of the sampling period. The correction is to 10°C. It will be observed that the "corrected" values give a much more consistent seasonal picture in the case of the succession series.

Analysis of variance of the corrected, undisturbed data for the ten plant types demonstrates significant differences between the plant types on each occasion whether based on the "between triplets" or the "discrepance" values.

To arrive at a realistic value for the pine soil it is probably best to add to the soil estimates (column 9a) a further amount to represent the

FIGURE 1.

The same data as in Table 1, corrected values only. Considerable differences between monthly values for grassland contrast with very consistent results in the succession series. The former perhaps linked with root activity and desiccation in June. Rank order within each series remains the same.



overlying litter. This, however, was inevitably disturbed when placed in the glass respiration vessels (see methods). As a rough indication, therefore, the correction factor of 0.54 can be applied to the litter measurements, giving values of 203, 169, 64 and 145 for the October, January, April and June samples respectively. These can be added to the soil figures to give totals of 434, 421, 355 and 341 units respectively. It may be noted that these considerably exceed the values for all the other sites, also that the seasonal pattern reflects that of seasonal leaf-fall.

If the seasonal pattern of the corrected respiration figures for the different vegetation types is examined it will be seen that, by eliminating temperature (which has been demonstrated by most authors to be the dominating determinant of respiration rate - see discussion) we are still left with rather a consistent seasonal pattern in the case of the grassland sites but not in the others. Various hypotheses come to mind. For instance the open meadows on sandy soil are subject to considerable desiccation which could well reduce both decomposition and root respiration in the summer months. On the other hand the April peak of activity might be connected with rapid root activity in April, a phenomenon which was also detected in a more thorough seasonal study in a grass area at Sesivangen (unpublished).

TABLE 2.

A comparison between undisturbed (U) and disturbed (D) readings taken in the ten vegetation types on successive occasions, 15 days apart (October/November 1976). Disturbed readings were from rings placed immediately prior to measurement. All figures are units of µl $CO_2/cm^2/hr$. To convert to $gC/m^2/year$ multiply by 20. These are the mean of readings at three adjacent positions (within 5cm.) and are corrected to $10^{\circ}C$. The vegetation area numbers are the five meadows followed by the Calluna succession series in the order listed in the text. Figures for site 9 (Pinus) apply to the soil fraction only.

Vegetation Area	1	2	3	4	5	6	7	8	9	10
Undisturbed	241	144	247	287	211	213	202	270	256	332
	272	142	188	185	219	225	267	349	240	311
	197	180	223	280	234	179	263	332	216	319
mean	236	155	219	250	221	205	244	313	231	320
Disturbed	382	226	360	484	424	383	416	533	389	682
	447	223	426	452	435	387	444	626	468	662
	379	301	359	495	433	402	492	680	453	628
mean	403	250	381	477	430	390	450	612	436	657
Ratio U/D	.58	.62	.58	.52	.51	.53	.54	.51	.53	.49

Table 2 provides the data of the "disturbance" experiment conducted in October/November 1976. Figures are the means from three adjacent respiration tubes corrected for temperature. It will be observed that the ratio of undisturbed to disturbed readings is rather consistent, despite the very different vegetation types with an overall value of 54%.

This figure is used to obtain an approximate value for the (disturbed) pine litter and is referred to in the discussion.

DISCUSSION

The Local Survey

The results shown in Fig. 1 and Table 1 do not indicate any significant difference among the grassland sites other than Kjællinge-Agre which is dominated by the pioneer grass Corynephrus canescens and which, as might be expected, has very low values. From this it appears that there was no detectable change in "respiration" between the three year and over six year fields.

On the other hand the series corresponding to a succession from Corynephrus via Calluna and shrubs to the woodland exhibits a three to four fold increase in "respiration" which is roughly ranked in the order of the above-ground biomass of the dominant vegetation. Subject to the reservations expressed below this would appear to indicate a reasonable relationship with primary production by the plants and serve as an encouragement to persue such methods especially in order to establish the productivity status of other plant communities in the region.

There is a considerable contrast between the seasonal patterns in the grassland as against the shrub and woodland sites, the former showing a uniform peak in April and decline again in June whilst the latter are much more consistent through the year. This is discussed below.

The General Validity of Soil Respiration techniques

This topic has been extensively discussed in the literature in which views on the usefulness of the technique vary from the optimistic (e.g. Coleman 1973a, 1973b, Lundgårdh 1927, Virzo de Santo et al 1976, Wanner 1970) to the guarded (Anderson 1973, Witkamp 1966a, 1966b, 1969) to the condemnatory (Minderman & Vulto 1973). The general relevance is discussed by Macfadyen (1976).

In principle carbon dioxide can be contributed to the soil from:

1. Decomposition of litter derived from above ground.

2. Decomposition of roots.

3. Respiration of "rhizosphere" organisms deriving nutrients mainly from "leakage" of soluble materials from roots.

4. Respiration of mycorrhiza whose carbon supplies are also derived from roots (see Harley 1973).

5. Respiration of the roots themselves - but less carbon dioxide translocated by the plant to above-ground parts (see Walter and Haber 1957).

Of these sources perhaps only the first two should be thought of as part of the decomposer industry of an ecosystem and only the last is unequivocally part of primary production. However it seems not unreasonable to consider the rhizosphere metabolism as part of decomposition and the mycorrhizal respiration as a symbiotic extension of the plant's physiology and thus to draw a line between items 3 and 4. The problem which has so far remained insuperable is to draw such a line in practice.

Further difficulties arise over losses of carbon as soluble components of the soil leachate and as carbon dioxide and other gases in the soil solution. Short term effects have also been postulated, and sometimes demonstrated involving expulsion of soil gases by changes in atmospheric pressure, water table etc.

The extent to which these problems invalidate "soil respiration" methods in practice clearly depends on the magnitude of the effects and the level of accuracy required in particular studies.

Perhaps one of the most useful attempts to quantify the problem is that of Chapman 1979, who worked in a Calluna heath and used a modelling approach similar to that of Douglas & Tedrow (1959). Chapman first used a respirometer which permitted repeated electrolytic titration within the covered vessel (1971) but later moved to terminal titration in a syringe (1976) which has the advantage of greater accuracy but is otherwise quite similar to the technique of the present study. His approach was to model the flows of carbon between the different compartments of roots, litter, root zone humus and sub root zone humus and to fit the results obtained by means of a regression equation. In this way he concluded that 70% of the total carbon dioxide emission was derived from the roots. He makes no separate estimate for mycorrhizae which, in the Danish heath were extremely evident by their fruiting bodies and which Harley (1973) has postulated to be capable of producing up to 30% of total soil carbon dioxide output. Presumably this source would in fact be included in the "root respiration" of Chapman's study. The approach of Bunnell et al (1975) is somewhat similar.

At the time of the Molslaboratory work the potential importance of mycorrhiza was certainly not appreciated and no estimate of their relative prevalence in different vegetation types was made: inasmuch as it is justifiable to regard them as part of the primary production component however this should not invalidate the results obtained and it could go some way towards explaining the very variable estimates of the importance of root respiration which have been published (from 17% by Coleman 1973b in successional grassland and oak forest, 35% by Edwards and Sollins (1973) in forest soil through 40% Kucera and Kirkham 1971 in prairie to 70% by Chapman (1979) and by Minderman and Vulto (1973) and by Wiant (1967) in forest soils.

Clearly, by far the most important factor limiting the usefulness of "soil respiration" is that of the proportion of carbon dioxide derived from "root respiration" in the broad sense of including mycorrhizal respiration. The most urgent need if the methods are to be extended is that greater insight should be obtained into the relative roles of roots in a range of ecosystems. This can be approached in a number of ways. Experimentally Witkamp (1966b) compared measurements in which carbon dioxide was prevented from moving between soil layers as did Edwards and Sollins 1973. Witkamp et al (1969) used other methods to physically separate the different components. Technical problems due to disturbance were not easily overcome in these studies but in general lower estimates of root respiration were arrived at. Physical separation of components and the use of a respirometer to determine root respiration in grassland was tried by Coleman (1973b) for old field and forest soils producing low estimates for root respiration whilst in grassland (1973a) he detected higher root activity. The extensive use of isotopic tracers for this purpose still appears to be an untried possibility.

In the meanwhile it is worth considering whether there is any value in these simple techniques as a primary survey method. It would appear from the present account that "spot" readings on a single occasion and without allowing for settlement, consistently give approximately double the estimate that would be obtained after a two week or more settlement period. Also that "correction" to a standard temperature permits some generalization from one occasion to a seasonal average. The fact that the seasonal pattern of the grassland readings contrasts so strongly with that in the other sites, may well indicate a major seasonal effect of root activity and even suggests that most of the "springtime peak" could be attributed to this factor whilst winter values represent decomposition only.

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QUESTIONS and COMMENTS

M.J. MITCHELL: How important is the solubility of CO_2 in water in affecting the utilization of CO_2 flux rates as a measure of soil metabolism?

A. MACFADYEN: I'm afraid I have not adequately considered this problem. Certainly there are many chemical and physical reactions which might influence CO_2 emissions. These should be studied in particular soils but I know of no qualitative as opposed to speculative data.

M. HASSALL: Please could you comment on the possible value of recent advances in soil sterilization techniques for isolating the contribution made by plant roots to the total soil metabolism.

A. MACFADYEN: I have not succeeded in that kind of technique although I have tried some. I hold out greater hope for tracer techniques in order to discriminate between carbon derived from the plant directly and that from decomposition.

B. AUSMUS: The length of equilibration and incubation greatly affects the variance and sensitivity of the measures. What did you choose to use and why?

A. MACFADYEN: I am afraid I misled you. The "incubation time" (i.e. the time of exposure of alkali) is one or two hours. The period of two weeks which I mentioned is the acclimatization time (the period during which open cylinders should be in the field before closure and absorption measurement).

M.S. GHILAROV: What is the contribution of soil animals to CO_2 evolution from the soil?

A. MACFADYEN: The best estimates of which I am aware indicate that the animals account for between 5% and 10% of the microbial respiration.

SESSION X: CLOSING

Moderator: Daniel L. Dindal

SUNY CESF, USA

SOIL ZOOLOGY COLLOQUIUM
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VII. ISSS
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r WORMS AND *K* WORMS: A BASIS FOR CLASSIFYING LUMBRICID EARTHWORM STRATEGIES

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UK

The development of the idea of dividing earthworms into two groups, surface-living red-pigmented forms and soil dwelling, non-red-pigmented forms leading to Bouché's (1977) classification into 'epigé', 'endogé' and 'anecique' life-forms is reviewed. It is suggested that the contrasting behaviour, morphology and physiology of the two forms represent evolutionary poles arising from r and K selection. Characters acquired in response to adaptive radiation into a variety of habitats are interpreted as secondary to those reflecting position along the r/K gradient.

Introduction: the development of an ecological classification of earthworms

The first recorded functional classification of earthworms appears to be that of Dame Juliana Berners, prioress of Sopwell Nunnery, who in 1485, in the first printed book on angling recommended as bait for eels 'the great angle twytch' and, for all other fish, 'red worms'. Little of further vermicological interest occurred until the late eighteenth century when Linnaeus (1758), O. F. Muller (1774) and Fabricius (1780) laid the foundations of modern earthworm taxonomy. After a further century, a basic edaphic distinction was drawn for the first time by P. E. Muller who in 1884 drew attention to the abundance of earthworms in mull soils and their absence, as he thought, from mor. The idea was notably expanded half a century later by his fellow countryman Bornebusch who in 1930 distinguished the lumbricid faunas of six types of soil and vegetation in Danish forests and heaths. Two of his most contrasting types were a) fresh mull soil with *Lumbricus terrestris, Allolobophora longa, Octolasium cyaneum, Allolobophora turgida, A. trapezoides, A. chlorotica* and *Eisenia rosea,* and b) beech raw humus with *Dendrobaena octoedra,* and more rarely, *Lumbricus rubellus, L. castaneus* and *Dendrobaena arborea.**

To this background of edaphic and distributional classification and their own studies on agricultural habitats, Evans and Guild in 1947-55 added extensive data on life histories and behaviour of the common species, distinguishing between a) the deep dwelling species which form well-defined burrow systems, cast on the surface or in soil spaces and generally aestivate during the summer, and b) the surface-dwelling non-burrow-forming species which neither aestivate nor form surface worm casts. Their data and his own observations were then summarized by Graff (1953) who divided the common lumbricids (Table 1) into a) red pigmented surface-living species, which occur predominantly in habitats with organic surface horizons, produce many cocoons, mature rapidly and may produce several generations in a year and b) those without red pigment which live in the mineral soil, occupy all agricultural habitats except compost, have a relatively low rate of cocoon production, mature slowly, aestivate and produce only one generation each year.

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*Throughout this paper, species names and spellings are those of the authors cited.

TABLE 1

Distribution and reproductive rate of common earthworms (from Graff, 1953)

	Arable	Grassland	Forest	Compost	Cocoons per year per worm	Hatching time (weeks)	Maturation time (weeks)	Offspring per year per worm
Red pigmented								
Lumbricus terrestris	++	++	+	0	41	10	50	35
Lumbricus rubellus	0	+++	++	+	94	10	40	80
Dendrobaena subrubicunda	0	+	++	++	95	4	15	110
Eisenia foetida	0	0	+++	+++	140	3	9	350
Not red pigmented								
Allolobophora caliginosa	+++	++	+	0	35	12	50	30
Allolobophora rosea	+++	++	+	0	21	12	50	18
Allolobophora chlorotica	+	++	0	0	31	7	29	27

The functional significance of the red pigmentation has been interpreted as a protective adaptation against injury by ultra-violet light (Zielinska 1913, Merker 1926a, 1926b); as a mechanism for controlling the extent of exposure during surface movement (Svendsen 1957 based on Hess1925); and as a cryptic adaptation to predation (Satchell, 1967b).

Perel (1975, 1977) emphasised the different feeding habits of the surface-living and burrowing types and within each distinguished three groups of species occupying different horizons.

During the 1950s and 60s, many further differences, morphological, behavioural and physiological, were demonstrated between the pigmented and unpigmented groups or representative pairs of them. Surface-living species were found to have a grasping tanylobic or closed epilobic cephalic lobe (Semenova 1966); pennate fibres in the longitudinal parietal musculature (Perel and Semenova 1968); to be small and mechanically unsuited to burrowing (Arthur 1965); to have a thin cuticle (Semenova 1968), a cylindrical intestine and a simple unfolded typhlosole (Semenova 1966). Soil dwelling species tended to be epilobic or proepilobic; to have bundle-like fibres in the parietal muscles; to be larger and to have a thicker cuticle, a beaded intestine and a folded typhlosole.

In general, the surface-living species, when compared with the burrowing species were found to be more tolerant of soil acidity (Satchell 1955; Laverack 1961); more sensitive to ultra-violet light (Stolte 1962); and more mobile over the soil surface (Svendsen 1957). Haughton *et al* (1958) demonstrated differences between *Lumbricus terrestris* and *Allolobophora terrestris* in the oxygen dissociation curves of the blood and Needham (1957) showed that *L. terrestris* excreted nitrogen at a substantially higher rate than *A. caliginosa*. Semenova (1967) observed that the chloragogenous tissue is unistratous in surface dwellers and multi-stratous in soil dwellers and considered that the ability to accumulate glycogen in chloragogenous tissue facilitated diapause.

In an important contribution on the respiration rates of earthworms, Byzova (1965) then showed that a more intensive metabolism is characteristic of litter dwelling and surface active species. She demonstrated first that the mean rate of oxygen consumption of pigmented species tends to be higher than that of unpigmented species of about the same size and that, in most pigmented species, oxygen consumption is strongly dependent on body size whereas in unpigmented soil dwelling species e.g. *Eisenia rosea* and *Allolobophora caliginosa*, the two parameters are only slightly correlated. In her discussion of these results, Byzova noted that the pigmented species with a higher metabolic level penetrate further to the North than non-pigmented ones, the distribution of *Dendrobaena octaedra* for example extending to the shrub tundra where under the prevailing conditions of low temperatures and short vegetation period it lives as an ephemeral.

A further distinction between the biology of the pigmented and unpigmented species was made by Satchell (1967) who used the data of Evans and Guild (1948) to show the striking relationship between the numbers of cocoons produced by the different species and the severity of their environments. For example, the deep burrowing non-pigmented species *A. longa, A. nocturna* and *Octolasion cyaneum* which are most protected from desiccation and temperature fluctuation produced 3-13 cocoons per annum whereas the pigmented *Lumbricus rubellus, L. castaneus* and *Dendrobaena subrubicunda* which live near the soil surface and are most exposed to heat, drought and predation produced 42-106 cocoons in a year.

Bouché's synopsis

From this background and his own field experience, Bouché (1971, 1972, 1977), has proposed an ecological classification of earthworms around three generalised lifeforms, "epigé, endogé and anecique". These are basically the surface-dwelling red-pigmented worms and soil-dwelling non-red-pigmented worms of earlier authors but distinguishing as anecics (from Greek, which come up) those species which have deep burrows but come to the surface to feed or defaecate. The characteristics of these groups can be summarized from Bouché (1977) (Table II).

An alternative interpretation

The system now proposed utilises most of the attributes listed by Bouché (Table II) and some others and suggests an evolutionary rationale for selecting them.

Selection pressures in earthworm evolution

Stephenson (1930) suggests that adaptive radiation in terrestrial annelids proceeded concurrently with the spread of the angiosperms in the Cretaceous. It seems likely, in view of the basically aquatic form of organization, that the first lumbricids were mud-dwellers, perhaps similar in habit and form to *Helodrilus occulatus*, with a low reproductive rate, low metabolic rate, low population density and low-grade organic matter as their food-source. From this form of organization it is perhaps a short evolutionary step to that of a soil-dwelling earthworm, a view consistent with that of other workers (Ghilarov 1949, Wilcke 1955) that the early lubricids were soil dwellers and that the main phylogenetic trend thereafter was to life on the soil surface.

Since the most nutritious and abundant food occurs in the surface organic horizons rather than in the mineral horizons, selection pressures seem likely to have favoured forms which could actively seek out and consume surface organic matter. Colonizing species would require a high metabolic rate sufficient to maintain the mobility required for food searching, and it would have been advantageous to develop sensory mechanisms for selecting these food sources and behaviour patterns serving to keep the population in their vicinity.

Organic horizons are best developed today in regions with severe winters, at high altitudes and at high latitudes in tundra and boreal vegetation. Colonizing earthworms in earlier epochs would have encountered similar habitats and their ability to exploit surface organic matter as a food resource would have depended largely on their success in surviving freezing. Huhta (1978) describes the effect on lumbricid populations of winter temperatures in Finland. Animals living in soil or litter were usually protected against low temperatures by snow but when this was thin or absent, populations of *Dendrobaena octaedra* and *Lumbricus rubellus* fell to 10% or less. These observations are consistent with those of earlier workers in the USA (Hopp & Linder, 1947) and Denmark (Larsen, 1949) who reported reduced population densities after cold winters, and with those of Bengston *et al* (1979) who found that *L. rubellus* and *A. caliginosa* survived in litter bags under 20 cm of snow in Iceland. Persson and Lohm (1977) found the biomass of *Dendrobaena octaedra* the same in winter as in summer, the worms moving downwards to a depth of 10 cm. Their site at 60° latitude was however much farther south than Huhta's. Ghiliarov (pers. comm.) reports that *Eisenia nordenskioldii*, known only from the Russian tundra (Matveyeva *et al*, 1975), survives freezing and at least a proportion of earthworms in northern latitudes, if acclimated, appear to survive temperatures down to about -3°C. At lower temperatures and in

TABLE II

Summary of characteristics used by Bouché to distinguish ecological types

	Epigeics	Endogeics	Anecics
Related to burrowing habit			
1. Burrowing muscles	Reduced	Developed	Strongly developed
2. Longitudinal contraction	Nil	Nil to feeble	Important
3. Hooked chetae	Absent	Absent	Present
4. Weight	Small (10-30 mg)	Small to large	Often large (adults 200-1100)
Related to surface habit			
5. Sensitivity to light	Feeble	Strong	Moderate
6. Response to irritation:	Positive	Positive	Positive
mobility	Rapid	Feeble	Moderate
7. Skin moistening	Developed	Slight	Strongly developed
8. Pigmentation	Homochromic (red brown or green)	Absent	Dorsal and anterior (dark brown)
9. Regeneration	Nil	Important (variable)	Important
Other characteristics			
10. Fecundity	High	Limited	Limited
11. Maturation	Rapid	Moderate	Moderate
12. Respiration rate	High	Feeble	Modest
13. Survival of adverse conditions	As cocoons	By quiescence	True diapause
14. Food size	Mesophage	Microphage	Macrophage
15. Intestinal transit	Slow	Rapid	Variable

populations not acclimated to freezing, few worms, if any, survive and populations overwinter as cocoons, - a strategy requiring the metabolic capacity to grow and reproduce rapidly during the favourable season.

Since surface feeding carries the penalties of exposure to predators, ultra-violet irradiation and desiccation it would have been advantageous to develop cryptic colouration, nocturnal surface activity, surface movement during rain, and means of moistening the respiratory surface with secretions. Tolerance to the acidity of many types of litter layer would also have been required.

As the group spread and competition for food intensified, adaptations to pioneer conditions will tend to have been replaced by new adaptations to survival on the lower grade food material of soil organic matter and by the return of the burrowing habit. Survival through the cold season below the soil surface creates the possibility of extending the life span beyond one season. A high biomass can then exist throughout the year ready to exploit the available food supply whenever temperature and moisture constraints permit. The need for rapid maturation and reproduction declines and the reduction in mortality from surface hazards reduces the rate at which cocoons must be produced to maintain the population density. Once the need to seek out a nitrogen-rich food source in order to produce a big seasonal batch of cocoons ceases, it becomes possible to conserve energy by reducing the rate of body metabolism and to adopt a more sedentary life.

By the operation of surface laws, reduction in metabolic rate permits an increase in body size and hence the power to form burrows. Subsurface feeding on soil organic matter can then be combined with feeding on surface plant remains from below or collecting materials on the surface close to burrow openings. Exclusively subsurface feeding patterns may also develop, including subsoil feeding. It then becomes prudent, so to speak, to maximise resource conservation by combining low metabolic rate with high longevity. Adaptive radiation into a variety of niches in both organic and mineral horizons could be expected to produce specialists in coprophagous, corticolous, subsoil, amphibiotic and other habitats.

It seems therefore that the Lumbricidae may have evolved from life in the soil to life on the surface and back again and that species with adaptations to soil dwelling are not necessarily older than species adapted to life on the soil surface. Wide differences in ecology between species in the same genus provide support for this view. *Eisenia foetida* and *E. rosea* and *Bimastos eiseni* and *B. muldali* show totally different modes of life as, according to Perel (1971), do *Dendrobaena attemsi* and *D. alpina*. Although revisions in nomenclature may eliminate some of these examples, others, for example in the genus *Lumbricus*, seem incontrovertible. Differentiation within species at the present time, e.g. in *Allolobophora chlorotica* (Satchell, 1967b) seems also to support the view that much of the adaptive radiation to be observed in the Lumbricidae is relatively recent.

In the northern hemisphere, the most important recent event in lumbricid evolution is the obliteration of the endemic populations of large areas by glaciation and the post-glacial recolonization of these areas by peregrine species. It can be inferred from the absence of post-glacial endemics that these events are too recent for new species to have evolved. Nevertheless, the changing selection pressures exerted on the existing stock of species as the tundra-like habitats of the immediate post-glacial period were succeeded by temperate ecosystems determined the species composition of the present-day lumbricids. Selection pressures favouring initially the short, fast life style of the surface feeder must have swung as the climate ameliorated to favour the slow, resource-conserving life-style of the soil dweller. The earthworm's answer to the question of whether it is better to live like a lion for a day or a lamb forever is, on this interpretation, partly historical and partly geographical.

Earthworm strategies as responses to r and K selection

It seems desirable in principle to harmonize ideas in soil zoology with concepts already established in general ecological theory. The division of earthworm life styles into these two basic types is paralleled by the concept of r and K selected species, already well established in evolutionary theory in 1967 by MacArthur and Wilson. The terms r and K are taken from the Verhulst-Pearl equation

$$\frac{dN}{dt} = r\ (1 - \frac{N}{K})\ N$$

where N is the population density
r is the intrinsic rate of natural increase
and K is the carrying capacity of the environment.
Discussing what happens to populations that invade island environments, MacArthur and Wilson coined the terms 'r selection' and 'K selection' to describe the different ways in which populations might function to survive in uncrowded and crowded environments. In an environment with no crowding, genotypes which harvest the most or the best food will rear the largest families and be most fit, evolution favouring productivity, but in a crowded environment, genotypes which can at least replace themselves with a small family at the lowest food level will win, the food density being lowered so that large families cannot be fed. Where climates are rigorously seasonal and winter survivors recolonize each spring in the presence of abundant food, r selection will operate favouring high productivity but where seasons are more uniformly benign , K selection favouring efficiency of conversion of food into offspring will result. Newly colonizing species will be subject to r selection but, once safely established will tend to become K selected.

While emphasising the importance of severe winters in generating r selection, MacArthur and Wilson explicitly recognized constraints on food and feeding as the crucial evolutionary pressure. Thus, in habitats with surface organic matter horizons and winter temperatures too low to permit feeding, r life strategies will be expected and where these horizons are lacking or transitory and soil becomes the main habitat, K strategies will prevail. In mediterranean or arid climates, the hot season imposes a similar constraint on earthworm feeding and only species which have evolved methods of combating desiccation survive. If a consequence of the hot season is an accumulation of surface litter and if this is not destroyed by fire but is available as food in the following wet season, r strategists may be expected to evolve no less than in high latitudes. But if the hot season accumulation of litter disappears before feeding is again curtailed by winter cold or summer drought, soil dwelling K strategies may be expected to prevail.

Southwood *et al* (1974) and Southwood (1977) discuss the stability of the environment as the arbiter of r and K selection, discontinuous distribution of food sources in space and time generating r selection. Stability in the earthworm environment is determined partly by food distribution but perhaps more importantly by variability in the conditions permitting feeding. Coprophogous and corticolous species encounter spatial discontinuity in the distribution of their food sources and litter feeders encounter seasonal fluctuations in supply. Soil organic matter provides a relatively stable food source and the soil environment is substantially buffered against the variations in moisture and temperature which limit feeding in surface-living species. Surface habitats tend therefore to be r-selecting and sub-surface habitats K-selecting.

Attributes of r and K life forms

Pianka (1970) lists a number of correlates of r and K selection (Table III) of which all but relative abundance (which does not apply to species but to groups of species) are relevant to r- and K-selected earthworms. There are unfortunately very few data available for earthworms on several of these correlates but in general there is a clear correspondence between the characteristics of surface-living pigmented species and of r selection and between those of burrow-forming, non-pigmented species and of K selection. Specifically, no data are available on mortality such as might show density dependance although Tomlin and Miller (1980) have shown in *Eisenia foetida* that growth and fecundity are related to population density. The pattern of survivorship is known for very few species but in *Lumbricus terrestris* it is undoubtedly of the type 3 pattern (Deevey (1947) with heavy mortality in early growth stages (Lakhani and Satchell, 1970) and in this respect it appears to be r selected. Population size, though perhaps rarely constant in any earthworm species, is apparently more constant in the burrowing than in the surface living forms, post-embryonic **stages** of *L. castaneus*, for example, disappearing entirely in some years during the summer (Bouché, 1977). No estimates have been made of the carrying capacity of earthworm environments, of the extent to which earthworm communities are saturated or of the intensity of competition. Recolonization each year by surface-living forms occurs in the sense that the population is annually replenished after reaching its seasonally lowest limits by a new generation of post-embryonic worms, soil-dwelling species maintaining post-embryonic populations through adverse seasons by vertical migration and quiescence. For the remaining characters in Table III the correspondence between surface-living worms and r selection and between soil-dwelling worms and K selection is generally well established.

Southwood (1977) has added a number of other concepts to this list. High levels of dispersal and fecundity, listed as attributes of r selection, are well-established characteristics of the surface-dwelling species as their converses are of burrowing species. Low and high levels of investment in defence and other interspecific competition mechanisms, listed respectively as r and K characteristics, may not be applicable to earthworms although it is too early to assert this positively until earthworm pheromones have been further investigated.

In discussion of body size, Southwood(1977) and Southwood *et al* (1974) interpret the large size of K-selected species as conferring survival advantage as a means of defence against attack. The idea of a retaliatory earthworm, however large, seems unsustainable despite the popular concept of the worm turning. A large worm attacked by a bird may lose a few segments and survive when a small worm would be consumed, nevertheless economy in energy metabolism and the mechanical capcity to burrow appear to be more important benefits of size. With some few exceptions attributable to the peculiarities of annelids, the characteristics distinguishing surface-living and soil-dwelling earthworms are not special to the group but are widely paralleled in similarly contrasting groups of r and K selected species throughout the plant and animal kingdoms.

As related to earthworms, the attributes distinguishing r and K lifeforms may be considered as those concerning reproduction and productivity; those related to the feeding behaviour associated with different levels of productivity, including adaptations to surface living or burrowing; and those which may be adaptive or may be associated with different metabolic rates as either causes or effects. They are summarised in Table IV.

TABLE III

Some of the correlates of r- and K-selection (Pianka 1970)

	r-selection	K-selection
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic, non-directed, density independent	More directed, density-dependent
Survivorship	Often Type III (Deevey 1947)	Usually Type I and II (Deevey 1947)
Population size	Variable in time, non-equilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecological vacuums; recolonization each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra & interspecific competition	Variable, often lax	Usually keen
Relative abundance	Often does not fit MacArthur's broken stick model (King 1964)	Frequently fits MacArthur model (King 1964)
Selection favours	1. Rapid development 2. High r max 3. Early reproduction 4. Small body size 5. Semelparity: single reproduction	1. Slower development, greater competitive ability 2. Lower resource thresholds 3. Delayed reproduction 4. Larger body size 5. Iteroparity: repeated reproduction
Length of life	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to	Productivity	Efficiency

TABLE IV Summary of attributes of r and K selected earthworms

A. Directly related to fecundity and length of life cycle:

		r	K
1.	Number of cocoons produced per worm	Higher	Lower
2.	Number of embryos produced per cocoon	Higher	Lower
3.	Incubation time of cocoons	Shorter	Longer
4.	Maturation time from hatching	Shorter	Longer
5.	Duration of reproductive life	Shorter	Longer
6.	Time distribution of mortality	Shorter	Longer
7.	Form of survivorship curve	Type III	Type I or II
8.	Seasonal stability of population density	Lower	Higher

B. Related to the feeding behaviour required to sustain different reproductive rates:

9.	Surface or subsurface dwelling	Surface	Subsurface
10.	Metabolic rate	Faster	Slower
11.	Mobility	Higher	Lower
12.	Sensitivity to pH	Lower	Higher
13.	Sensitivity to light	Higher	Lower
14.	Pigmentation	Pigmented	Unpigmented
15.	Avoidance of desiccation	Quiescence	Diapause
16.	Size	Smaller	Larger
17.	Morphological adaptations to burrowing	Poorly developed	Well developed
18.	Form of prostomium	Tanylobic	Epilobic or proepilobic
19.	Form of typhlosole	Smaller, unfolded	Larger, folded

C. Related to metabolic rate

20.	Nitrogen excretion rate	Faster	Slower
21.	Intestinal transit rate	Faster	Slower
22.	Oxygen affinity of haemoglobin	Lower	Higher

Characters not included in this list but noted by Bouché (Table II) include food size and response to irritation. Insufficient published data is available on either of these to permit their inclusion. Field observations of responses to vermifuges are difficult to interpret because size of burrow openings and other confounding factors affect vermifuge penetration. More direct data are needed.

Intestinal transit rate is also difficult to interpret. Like nitrogen excretion rate it may have adaptive significance or it may be a function of metabolic rate. The characteristics of the haemoglobin may also distinguish the two extremes of life form but interpretation of its significance awaits evidence from additional species.

Avoidance of desiccation in the surface feeding species is facilitated by their high mobility, their habit of moving during rain showers and to some extent by nocturnality. Summer diapause occurs in endemic species of regions south of the limits of glaciation and perhaps evolved much earlier. The regeneration of lost segments during diapause seems of doubtful ecological significance although Bouché (1977) considers it an adaptation to predation.

Adaptive radiation within r and K strategies

Within the confines of the r strategy several variations in life style are possible (Table V). *Dendrobaena octaedra* and *Bismastos eiseni*, living in forest or heathland litter layers are seen as predominantly r-selected. *Lumbricus castaneus* occurs in litter layers but more abundantly in grassland where it is adapted to exploitation of ephemeral dung pats. *Eisenia foetida*, originally a corticolous litter-layer species (Graff, 1974) is now also adapted to man-made habitats in nitrogen-rich organic matter. *Lumbricus rubellus*, primarily an r strategist, lives in forest litter or in grassland as a partial coprophage. In some sites with a thin litter layer it burrows into the mineral soil and seems part way along the route to a K strategy. *Lumbricus terrestris*, further along the same route, has the reproductive features of a K life form but, having retained the r selected habits of feeding and mating on the surface, also retains the pigmentation of the r strategist. *Eiseniella tetraedra* is perhaps an r strategist that has become semi-aquatic.

Predominantly K-selected types are *Allolobophora caliginosa*, living in the A horizon of mull soils, reproducing slowly and maintaining a high biomass throughout the year, and *Eisenia rosea* with similar habits. *Allolobophora chlorotica*, also a mull soil dweller, lives just below the soil surface where it is much exposed to bird predation. Its pigmentation, thought to have cryptic value, is of an entirely different composition (Kalmus, Satchell and Bowen 1955, Satchell 1967b) from that of r strategists. *A. longa* and *A. nocturna* are two typical K strategists which in their exploitation of the full depth of the A horizon have developed the behaviour of defaecating on the surface. Their distal pigmentation is also of a different composition from that of r strategists. *Octolasion cyaneum* and *O. lacteum* are K strategists adapted to exploitation of permanently moist subsoil. The latter has a weak ability to diapause but is enabled by a well-developed network of subcutaneous blood vessels and a high concentration of haemoglobin to inhabit poorly aerated soils (Perel, 1977).

TABLE V Adaptive radiation of some peregrine earthworms

	← r				K →
Surface feeders					
Litter layers	*D. octaedra*				
Litter and subcortical	*B. eiseni* *D. subrubicunda*				
Litter and dung pats	*L. castaneus*				
Litter and dung heaps	*E. foetida*				
Surface and subsurface feeders					
Semi-aquatic	*E. tetraedra*				
Litter, dung pats and subsurface		*L. rubellus*			
Litter and soil organic matter			*L. terrestris*		
Subsurface feeders					
Surface soil				*A. chlorotica*	
Soil organic matter and litter					*A. nocturna* *A. longa*
Soil organic matter					*A. caliginosa* *E. rosea*
Aquatic muds and subsoil					*H. oculatus* *B. muldali*
Subsoil					*O. cyaneum* *O. lacteum*

Within the main divisions of r and K strategists, many forms of adaptive radiation are thus seen to be possible and this can be expected to apply also to endemic species. Where winter temperatures or summer drought do not permit survival of post-embryonic worms r life-forms may be expected, - where adult or juvenile worms can survive throughout the year, a variety of adaptations within the K life form will occur.

In the Megascolecidae, Lavelle (1979) found that small species living close to the surface have a high multiplication rate and are the most productive (P/B) and the least efficient (P/I) and that large species living deep in the soil are less productive and more efficient. It seems therefore that although some divergence may be found from the suites of r and K attributes appropriate to the Lumbricidae, the Megascolecidae and possibly other earthworm groups may also be capable of analysis in terms of r and K selection.

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QUESTIONS and COMMENTS

M.B. BOUCHE: Just a remark about resistance by cocoons. When I discovered this phenomena (in *Lumbricus castaneus* Savigny) that was not during the cold season but in dry summer. To the best of my knowledge until now resistance by cocoons is the equivalent of quiescence or diapause during drought.

J.E. SATCHELL: Yes, thank you. Although I have developed the theme of r-selection in earthworms primarily in relation to colonization of regions with cold climates, it could also be developed in relation to the seasonally available resources in hot climates. Cocoon survival through dry summers would then be equivalent to cocoon survival through cold winters as one of the means by which populations persist through adverse seasons.

M.S. GHILAROV: You have pointed out that earthworms cannot survive freezing. But *D. octaedra* and *E. nordenskioldii* do survive such freezing which is line vitrification.

J.E. SATCHELL: It is true that some earthworms can survive freezing in the extreme northern limits of their range and this may be by acclimation in for example *D. octaedra* or, possibly an evolutionarily recent adaptation in *E. nordenskioldii*. The point is not critical however since even in these species they appear to suffer a severe reduction of population in the winter. r-selection will therefore operate to favour a high rate of population recovery in the spring.

M.S. GHILAROV: You suggest that there are quite different evolutionary trends in colourless and pigmented Lumbricids. But *Eisenia nordenskioldii* is found invariably pigmented as well as colourless in some localities.

J.E. SATCHELL: In general the more K-selected geophagous species are less pigmented than the more r-selected species. However, polymorphic species can be found exhibiting interspecific differences in relation to the r-K gradient. *Allolobophora chlorotica* may be interpreted in this way as having a green pigmented form which is perhaps more r-selected than the K-selected unpigmented form.

M.S. GHILAROV: Earthworms were often found in winter in frozen soil layers. They can be in the overcooled state and even active in the "vitrified" soil, as M.N. Gorizontova, L.A. Krasnaya and T.S. Perel (Uchenye Zapiski Moskovskogo Gorodskogo Pedagogicheskogo Institute, LVI: 161-178, 1957) have observed near of Moscow on *Lumbricus* sp. (juv.) and *Nicodrilus caliginosus*. But they can also be quite frozen as B.A.Tichomirov (Priroda, No. 5, 1957) observed on Novaya Zemlya. There were also old records of living earthworms frozen into the ice (I. Recker, Zool. Cluz. Bd. 19:3-4, 1896; E. Sekera, ibid. 159). There are also some data on "vitrification" of earthworms, but not correctly analyzed.

SOIL FAUNA STUDIES FOR SOLVING PROBLEMS OF BIOGEOGRAPHICAL CONNECTIONS

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Soil animals are exclusively appropriate to elucidate biogeographical as well as paleogeographical connections of various territories, principally those taxonomic groups, with representatives that have feeble potencies to dispersal. Of especial interest with this respect are earthworms, woodlice, millipedes, centipedes and higher insects whose larvae develop in the soil whereas imagines are not or are little capable of flight. Actively flying insects and various invertebrates adopted to anemochory or ornithochory are of minor value for solving biogeographical problems.

Certainly biogeographical problems are to be solved when studying territories minimally influenced by man where the possibility of anthropochory is practically excluded. Some examples taken from the author's own experience are as follows.

In the red-coloured soils on limestone rocks of the South Crimea coast the majority of larger soil invertebrates belongs to species distributed in the Mediterranean, especially in the East-Mediterranean area whereas in other soil types in the same locality Mediterranean species do not occur or their percentage is many times lower.

As examples, typically Mediterranean species may be found such as Haploembia solieri Ramb., Dilar turcicus Hag., Licinus silphoides Rossi, Ophonus subquadratus Dej, Blaps mucronata Latr. and many others common to the Crimean red soils. As such species do inhabit "terra rossa" in the Mediterranean province, red-coloured soils of the South Crimean coast are to be identified as nowadays forming "terra Rossa" (Ghilarov, 1956), because their regime corresponds to ecological demands of various Mediterranean soil invertebrates, which proves that these soils are the result of the contemporary soil formation. This excludes the assumption of some pedologists that Crimean red soils are fossil ones exposed by erosion.

These data prove also that ancient, already disappeared, land connections of the South Crimea with Asia Minor and the Balcan peninsula occurred in the Tertiary.

Another example is the study of "bald summits" of calcareous mountains in the North-West Caucasus situated above the belt of beech and oak forests (altitude 800-1100 m). These summits are covered with steppe-like vegetation cover (Stipeto-Festuceta or Festuceta herbosa) and the soil fauna there is very similar to that in steppes of the Ukrainian plains. Such a group as tenebrionids is represented by *Opatrum sabulosum* L., *Pedinus femoralis* F., *Oodescelis polita* Sturm., and *Cylindronotus breviocollis* Kust; though each of these species may not be regarded as an indicator of steppe conditions, the combination of species of this "taxocenose" is characteristic of steppes. The same is true for Scarabaeidae-Pleurosticti (*Amphimallon solstitiale* L., *Rhizotrogus aestivus* Ol., *Rhizotrogus aequinoctialis* Herbst, *Pentodon idiota* Herbst). And the typical steppe genus *Dorcadion* was represented by *D. caucasicum* Kust.

Such ground beetles as *Zabrus spinipes* F., and *Harpalus flavicornis* Dej. or such weevils as *Otiorrhynchus fullo* Schrnk., *Stomodes tolutarium* Boh., *Brachycerus junix* Licht. are common to Ukrainian virgin steppes, though being of the Mediterranean origin.

The cockroach (*Ectobius duskei* Adel.), the japygid (*Confusus rumaenus* Silv.), the millipede (*Chromatoiulus rossicus* Tim.), the centipedes (*Escaryus retusidens ornatus* Folkm., and *Clinopodes flavidus escherichii* Verh.), the sowbug *Protracheoniscus giliarovi* Borutzki) and others are typical to plain steppes of the steppe zone (Ghilarov and Arnoldi, 1969). The occurrence of such species with a negligible potency to dispersal shows the relic and not a secondary character of these mountain steppe ecosystems; the penetration of these steppe elements upward into the mountain through the forest belt is quite improbable. Not only steppe vegetation but also the whole ecosystem of the studied summits prove their immediate connection with plains in the xerothermic period before glaciation.

A soil faunal study was presently applied also to solve the problem of the history of some juniper forests inside the Transcaspian Desert.

In this desert (West Turkmenia) the western branches of the Kopetdag Mountain range are ending. This range is now connected with other mountain systems of the Central Asia.

To the northwest from Kopetdag separated from it by the very dry Karakoum Desert there are two isolated small mountain ranges - the Small Balkhan and more remote and the higher (alt. 1880 m) Big Balkhan. The southern slope of this last range is covered with desert vegetation whereas on the steep northern one there are Junipereta. Junipereta in West Turkmenia represents isolated arboreal communities in mountains and are considered as those of humid type (Korovin, 1961).

Northwestward from Kopetdag the northern slope of Big Balkhan is the only site where juniper forests are growing (surrounded with desert vegetation). On a steep slope undergoing erosion, if growth conditions are favourable for the edificator plant species, it is rather arbitrary to draw a conclusion whether the vegetation cover is of a recent origin (due to the possible passive transportation of seeds by wind or birds) or of an ancient relic one. In the case under study the arboreous juniper species both on the Big Balkhan and on the Kopetdag northern slopes is *Juniperus turkomanica*, which is rather close to a more occidental one - *J. polycarpos* growing in Transcaucasus, whereas eastward in Tien-Shan Mountain system it is substituted by *J. turkestanica*. To solve the nature and age of Big Balkhan Junipereta the data on soil fauna composition are of real interest.

In the Junipereta of Big Balkhan many soil animal species were found common to Kopetdag Junipereta too. Such are e.g. the earthworm *Allolobophora persiana* Mich., described from Iran, centipedes *Lithobius icis* Zalesskaya, known only from Big Balkhan and Kopetdag Junipereta and *Henia bicarinata* Mein., found during our many decades of studies in juniper forests of Kopetdag, the Transcaucasus, the South Crimean and the Northwest Caucasus. Only in the Junipereta of Big Balkhan and of Kopetdag a new species of *Pachymerium* was found which is yet to be described.

In Big Balkhan there was found the ground beetle *Dyschirius beludsha* Tschitasch., described from Beludjistan. *Cockchafer* (*Miltotrogus*) *aschhabadensis* Nonv. and its white grubs were sampled both in Big Balkhan and Kopetdag under juniper cover.

Such tenebrionids as Zophohelops steinbergi G. Medv. and Z. arvatensis G. Medv., described and known from Kopetdag only, were found also in a Juniperetum of Big Balkhan. The same concerns also Blaps seriata F.-W. and the ant, Aphaenogaster fabulosa K.Arn.

All these species are to be regarded as mesophilous elements of the soil population common to Junipereta in West Turkmenia, absent under the xerophilous vegetation in surrounding deserts.

Korovin (1961) indicates that the penetration of the Junipereta into the Middle Asia occurred in the Tertiary.

The occurrence in the Junipereta of Big Balkhan of the above mentioned soil animal species common to Kopetdag (and in some cases also to Khorasan, Elburs and the Transcaucasus) proves the ancient (Tertiary) connections of juniper forest biocenoses of Big Balkhan with those of Kopetdag and other southern territories (Girkan province).

Such connections could not have been established in the dry Quarternary. Beginning from the early Paleocene, Big Balkhan was a territory, acquiring during the sea transgressions an insular position.

With this peculiarity of the history of Big Balkhan the existence of many endemics (not mentioned in this communication) is connected.

But mesophilous soil faunal species common to Big Balkhan and Kopetdag prove that there were ancient immediate relations of these mountain ranges dating from the early Miocene. In the Mesozoicum the whole territory of the contemporary Transcaspian Turkmenia was under the sea. In the Eocene, Big Balkhan was an isle. And in the early Miocene there was a sea regression, and there was an immediate land connection between Big Balkhan and Kopetdag. In the late Miocene a new sea transgression (the Sarmatian one) took place; Big Balkhan and Kopetdag became isles. In the upper Pliocene (Akchagyl transgression) the aquatic innundation became still greater. In the Quarternary there was established a dry desert climate, and the land bridge between the mountains of Big Balkhan and Kopetdag was unsuitable for the distribution of mesophilous soil animals. But evidently of the Quarternary origin, some

Big Balkhan dry summit inhabiting rodents are known in this country besides only from Kopetdag and partly inhabiting Transcaucasia (Ochotona rufescens Gray, Meriones persicus Blanf, Ellobius fuscocapillus Blyth. and others).

Thus during early Miocene was the only geological period when there were possibly an immediate connection and exchange between mesophilous soil faunal elements of Kopetdag and Big Balkhan Junipereta. This is just the period when representatives of the genus Juniperus supposedly invaded the territory of Middle Asia.

The existence of mesophilous soil faunal complexes common to the Big Balkhan and Kopetdag (as well as Elburs and other areas) proves this that Big Balkhan was surrounded by sea during the other periods of the Tertiary. Therefore, from the biogeographic viewpoint it is clear that it is necessary to appreciate the western limits of the mountain system of Middle Asia not as coinciding with those of Kopetdag, as it is generally accepted (Gerasimov, 1968), not with Small Balkhan as it was suggested by L.S. Berg (1952), but ending with Big Balkhan.

These data show that soil faunal studies do help to solve some difficult problems of historical biogeography.

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QUESTIONS and COMMENTS

M.B. BOUCHE: When was the last (i.e. the most recent) biologically possible contact between the group of Balkhan and the Kopetdag mountains?

If that means a separation since around 13 million years ago (13 M.A.) I am surprised, at least for the earthworm *Allolobophora persiana* by the absence of morphologically noticeable divergent evolution. As you know (my book 1972), I prove a close relation between historical area pattern and systematic hierarchy. For instance, the genus *Scherotheca* split off into two subgenera around 60-40 M.A. (opening of Biscayne Bay); in the subgenus *Scherotheca* (*Scherotheca*), a species (*S. dugin*) differentiated in the French Alps, and these mountains formed in the Miocene (13 M.A.). In turn, this last species migrated later to Corsica thanks to a short event - the drying up of the Mediterranean Sea (6 M.A.). Today a peculiar subspecies is clearly differentiated in Corsica (*S. dugin brevisella*). So, I think it is strange that an earthworm species could remain unchanged (without divergence) since Miocene.

M.S. GHILAROV: Though the territory of Big Balkhan and Kopetdag separated in the Miocene, the territorial conditions were very similar. The distribution of the Juniperata in Middle Asia is dated from Miocene, and probably the whole community is developing quite parallel. Existence of endemic Big Balkhan species related to those of Kopetdag prove that in some cases changes did occur e.g. the occurrence in the South Crimea of *Haploembia solieri*, a species of older times which had no possibility of later invasion.

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